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An investigation of non-spatial cognitive abilities in an asocial corvid, the Clark's nutcracker (Nucifraga columbiana)

Jan K. Tornick
University of New Hampshire, Durham

AN INVESTIGATION OF NON-SPATIAL COGNITIVE ABILITIES IN AN ASOCIAL CORVID, THE CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA*)

BY

JAN K. TORNICK

B.S., Ramapo College of New Jersey, 2003
M.S., University of New Hampshire, 2007
M.A., University of New Hampshire, 2009

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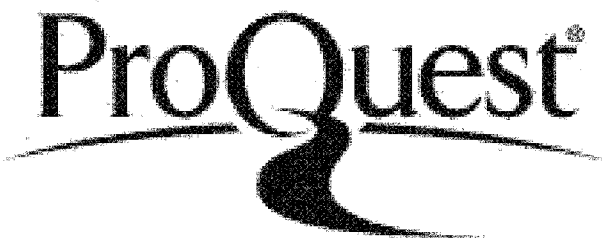

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This dissertation has been examined and approved.

Dissertation Director, Brett M. Gibson, Associate Professor of Psychology and Neuroscience and Behavior

Robert G. Mair, Professor of Psychology and Neuroscience and Behavior

Robert C. Drugan, Professor of Psychology and Neuroscience and Behavior

Michelle P. Scott, Professor of Neuroscience and Behavior and Zoology

Winsor H. Watson III, Professor of Biology and Marine Sciences and Neuroscience and Behavior and Zoology

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Date

DEDICATION

To Artz, Fitz, Sony, Puck, Starr, Betsy, and Susan. Thank you.

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University of New Hampshire, May, 2012

A great deal of research suggests that the cognitive abilities of birds in the family Corvidae (crows and jays) are comparable in many aspects to that of apes. Scientists have posited competing hypotheses to explain how complex cognitive abilities arise in a species or group of animals. One such hypothesis, the social-intelligence hypothesis, states that the demands of living in a large, dynamic group drive an animal's need for complex cognitive skills. Another, the ecological-intelligence hypothesis, predicts that generalist foragers develop more highly flexible behaviors and a wider cognitive repertoire than specialist foragers. To date, cognitive research on corvids has focused on corvids that are highly social and are generalist foragers. From a comparative standpoint, I examined the cognitive abilities of a corvid that is relatively asocial and a specialist forager. The Clarks' nutcracker (*Nucifraga columbiana*) is thought to be perhaps the least social corvid, and it largely specializes on the seeds of one species of pine (*Pinus edulis*). I tested nutcrackers using several tasks, in three broad areas of cognition: inferential reasoning, numerical discrimination, and social intelligence. These experiments represent novel tests of cognitive abilities in this species. I found that the nutcrackers performed in a similar manner as social mammals and corvid birds, in all three areas of cognition. This

suggests that social group size may not have a large impact on the development of a broad range of problem solving skills. Rather, ecological pressures associated with finding, extracting, caching and protecting seeds from pilferage may have influenced the development of complex cognition in this species.

CHAPTER I

BACKGROUND AND PURPOSE

Cognition in Corvids

A number of recent studies suggest that members of the family Corvidae (also 'corvids', relatives of the crows and jays) have cognitive abilities that seem to surpass many other groups of birds, and are surprisingly similar to primates (Emery & Clayton 2004). Comparative psychologists are interested in members of the corvid family because many species of corvids possess several of the characteristics considered important for advanced cognition, such as a large and complex social structure, mostly generalist foraging, a relatively large brain, and altricial young (Emery 2006). The corvid family is comprised of over 120 species, a third of which fall within the genus *Corvus* (jackdaws, crows and ravens) (Madge & Burn 1994). Many species of corvids are highly territorial, protecting territories either all year or only during the breeding season. Some corvid species roost communally, in very large groups of up 65,000 individuals (i.e. rooks *Corvus frugilegus*, Patterson et al. 1971). Others, including the jackdaw (*Corvus monedula*), also nest communally. Many form partner-bonds which are extremely strong, and in some cases are lifelong. Males often provision females during gestation and sometimes help with brooding the eggs; they may also help the females feed the helpless young. Some members of the corvid family breed cooperatively; that is, there are additional adults (usually older siblings) that help raise the nestlings (Goodwin 1976).

Furthermore, like monkeys and apes, corvids often have a strong dominance hierarchy within a group (Emery 2006). These characteristics make corvids a good model to compare with primates for insight into how convergent evolution may act to produce similar features (like complex cognitive traits) in distantly related organisms.

Empirical studies with corvids suggest that they indeed possess many aspects of cognition previously ascribed only to humans and our close relatives (for review see Emery & Clayton 2004), such as an understanding of Piagetian object permanence (Pollok et al. 2000, Zucca et al. 2007, Salwiczek et al 2009), gaze following (Schloegl et al. 2007, Schloegl et al. 2008), transitive inference (Bond et al. 2003, Paz-y-Mino et al. 2004), planning for the future/episodic-like memory (Clayton & Dickenson 1998), and tool use (Heinrich 1995, Hunt & Gary 2006, Hunt et al. 2006, Kenward et al. 2005). For example, New Caledonian crows (*Corvus moneduloides*) manufacture sticks and leaves into hooks and other regularly-shaped instruments. These are not crude tools; the birds actually sharpen and refine the tools with their bills, making wide, narrow and stepped type tools. They have a wider range of variety in their tools than any other species known, except humans. The design of these tools also shows evidence of evolution through diversification and cumulative changes (Hunt et al. 2006). In the laboratory, naïve juvenile New Caledonian crows also spontaneously fashion tools out of materials that they have never encountered before (Weir et al. 2002, Kenward et al. 2005). Remarkably, they can even use tools to manipulate other tools (meta-tool use), a skill which only humans and perhaps a few primates were thought to possess (Taylor et al. 2007). Other species of corvid also use objects in goal-directed tasks. American crows (*Corvus brachyrhynchos*) drop objects on humans to protect their nests and offspring

(Caffrey 2001). In addition, both American crows and Steller's jays (*Cyanocitta stelleri*) have been observed using a pointed twig in a weapon-like manner in a competitive feeding situation (Balda 2007).

Another line of research that demonstrates the extraordinary mental capacities in corvids is the study of episodic-like memory. Episodic memory in humans has been defined as a record of a person's experience that holds temporally dated information (Tulving 1984). These records include the precise memory of "what", "when", and "where" for personal events that occurred in the past; furthermore, evidence of conscious recollection must be present. Clayton and Dickinson (1998) provided evidence that scrub jays (*Aphelocoma californica*) may possess episodic-like memory. The authors coined the term "episodic-like" because their research did not address phenomenological aspects of episodic memory. In the study, scrub jays remembered where they cached different food types and recovered them according to the perishability of the item and how long it had been since caching. Scrub jays appear to remember the "what", "where", and "when" of a caching event. Primates tested in the same manner show a similar pattern of results. Such performance meets Tulving's criteria for episodic memory. However, critics have argued that nonhuman animals can only act based on immediate needs, as opposed to future needs. This is known as the Bischof-Köhler hypothesis (1985). To test the Bischof-Köhler hypothesis, Correia and colleagues (2007) demonstrated that scrub jays selectively cache different types of food depending on which type of food they will need at a future time. These findings provide evidence against the Bischof-Köhler hypothesis because the scrub jays flexibly adjust their behavior based on future needs. These and other discoveries have prompted scientists to explore complex cognitive abilities that

corvids (and other intelligent birds like parrots) might have in common with primates. Examination of multiple cognitive processes in birds may undermine the long-held notion that only primates possess advanced cognitive abilities.

Clark's nutcrackers

The Clark's nutcracker (*Nucifraga columbiana*) is a member of the corvid family of birds. Recent nucleotide sequence data for the family Corvidae (Ericson et al. 2005) suggest that nutcrackers are phylogenetically most closely related to crows and rooks (genus *Corvus*). In addition, phylogenies which were reconstructed based on social behavior (Ekman & Ericson 2006) and caching behavior (deKort & Clayton 2006, Ekman & Ericson 2006) also seem to concur that nutcrackers and crows shared a very recent common ancestor. If these species did evolve from a common ancestor, then they may share complex cognitive abilities (see above for examples). The nutcracker, however, possesses several unique ecological characteristics compared to other members of the corvid family.

The nutcracker is a seed-caching corvid that lives in alpine regions of North America. It inhabits perhaps the harshest environment of all the corvids, living mostly at altitudes of 900–3,900 meters (3,000–12,900 ft) in high arid pine forests. The nutcracker is a specialist forager (unlike most generalist corvids) that depends largely on the seeds of one species of pine (*Pinus edulis*). These birds cache and recover an estimated 33,000 pine seeds each autumn (Lanner 1996). As many as 2500 caches of 5-10 seeds are stored over an area of up to 20 square kilometers (13 square miles) (Balda & Kamil 2006). Research suggests that they are able to recover up to 90% of the cached seeds (Balda & Kamil 2006), which they rely on as their principle energy source over the harsh winter.

Surplus seeds often germinate and grow into new trees; thus the nutcracker is an important part of the ecology of the pine forest it inhabits. Nutcrackers relocate their caches with remarkable accuracy up to six months later, even under a meter (3 ft) of snow (Lanner 1996). To be able to do this, they must keep track of temporal and spatial cues to find seasonal seeds that are sensitive to decay. In fact, the nutcracker has become a textbook model of spatial memory and navigation; many studies have demonstrated its extraordinary spatial learning abilities. Nutcrackers seem to relocate their caches by developing a mental map of landmarks in their environment. Then they recall the location of the caches relative to these landmarks (Kamil & Balda 1985, Gibson & Kamil 2001a and b, Gibson & Shettleworth 2003). This "mental map" may help them to plan the most efficient routes between caches (to conserve energy). Research shows that nutcrackers have better spatial memory than related corvids that do not depend as heavily upon the recovery of food caches during the winter (Gibson & Kamil 2005). Although a great deal is known about spatial cognition, very little is known about other types of cognition in this species.

The nutcracker is the least social of the corvid family (Templeton et al. 1999). It does not live in large flocks like some other corvids, nor does it nest cooperatively. Clark's nutcrackers are monogamous, forming long-term pair bonds. The pairs stay together on their territories all year and nest in late winter (Mewalt 1956). Both males and females jointly build the nest, incubate the 2-5 eggs, and feed the juveniles. The young remain with the parents until they are about 4 months old, during which time they learn about the intricacies of caching behavior (Lanner 1996). It is not yet known whether nutcrackers exhibit some of the social cache-protection strategies seen in other corvids.

Conspecifics are known to pilfer caches (Bednekoff & Balda 1997, deKort et al. 2005). However, it is not clear if nutcrackers cache fewer seeds or re-cache their seeds in new locations if they are observed by a conspecific, like the more social scrub jays (Dally et al. 2005a).

Social- and Ecological-Intelligence Hypotheses

Comparative and evolutionary psychologists seek to understand the environmental conditions that are responsible for the evolution of a cognitive trait. Several different hypotheses about these conditions have been proposed. For example, the "social-brain" hypothesis posits that animals living in large groups evolve a proportionally larger forebrain, an area which controls complex cognition and attention (deWaal 1982, Barrett et al. 2002). Another, the "social function of intellect" hypothesis (also called Machiavellian intelligence hypothesis, Byrne & Whiten 1988) suggests that animals develop a larger cognitive repertoire in response to challenges associated with social complexity (Humphrey 1976, Jolly 1996). Organisms that are exposed to complex social interactions (involving skills like keeping track of dominance hierarchies and altruistic acts, formation of coalitions, etc.) may have evolved superior problem solving skills; and individuals with exceptional skills may have had higher reproductive success (Owen 2009). To examine the effect of sociality on "intelligence", Jolly (1966) examined problem solving in several species of lemurs (a prosimian primate that is less social than other primates) by exposing them to wide variety of cognitive tasks ranging from object permanence to "insight" problems (i.e. opening boxes and pulling strings). The results indicate that the lemurs' performance falls below that of other primates. Thus, Jolly posits that the structure of primate society may have been the driving force for the

evolution of primate intelligence. Both Jolly (1966) and deWaal (1982) believe that additional research is needed to examine whether correlations exist across species between social complexity and individual "intelligence".

Other scientists have hypothesized that complex cognitive traits arise (as adaptive specializations) for coping with ecological problems associated with foraging. For example, the "ecological-intelligence" hypothesis predicts that generalist foragers develop more highly flexible behaviors and a wider cognitive repertoire than specialist foragers (Altshuler & Nunn 2001). Advanced cognitive skills, like memory, planning, and complex food extraction strategies, could have been favored among animals that utilized resources in new ways. The "extractive foraging" hypothesis posits that difficulty extracting food from its casing may have driven the need for complex intelligence (Parker & Gibson 1977, Gibson 1986). The "ephemeral food supply" hypothesis states that utilizing food sources that are scarce or seasonal may lead to an increase in cognitive capacity (Clutton-Brock and Harvey 1980, Milton 1981). The "cognitive mapping" hypothesis suggests that locating patchily distributed but predictable food sources may drive complex cognition, due to the need for a mental representation of the environment (Milton 1988). In all of these models, more efficient foraging may have led to increased inclusive fitness (Owen 2009). Unfortunately, much of the evidence supporting these hypotheses is anecdotal, and empirical studies aimed at specifically testing them have been rare. This is especially true in groups other than primates.

Purpose

The overarching goal of this research was to examine social intelligence hypotheses, by conducting comparative experiments on a species of bird that is relatively

asocial. If social group size is an important predictor of complex cognition, then the asocial nutcrackers' performance on many cognitive tasks should fall below that of more social mammals and birds. Alternatively, evolutionary pressures related to foraging may promote the development of certain cognitive traits (adaptive specialization). If ecological pressures from finding, storing, retrieving, and protecting food influence the development of a particular cognitive trait, the nutcrackers' performance on a wide variety of cognitive tasks should be similar to that of closely related corvids that also cache food. The nutcrackers' performance may also be similar to that of distantly related animals whose ancestors faced similar socio-ecological pressures, and may have derived similar cognitive traits through the process of convergent evolution. This research allowed me to compare the performance of the nutcrackers on several tasks with that of primates and other corvids, to address potential hypotheses regarding the evolutionary origins of cognition in corvids.

In this body of work I examined the nutcrackers performance on tests in three broad types of cognition: 1) inferential reasoning by exclusion, 2) numerical cognition, and 3) social cognition. In the first study, I examined inferential reasoning in the nutcrackers, to determine if sociality drove the need for complex reasoning abilities (like the ability to make inferences) that have been demonstrated in social mammals and birds including corvids. If sociality is important, the nutcrackers should not demonstrate the ability to reason using inference, like ravens and other more social caching corvids and highly social mammals that have been previously tested. Alternatively, if other evolutionary pressures (like keeping track of food) drove the need for complex reasoning abilities, the nutcracker should demonstrate the ability to reason using inference (like

ravens and other caching corvids), and other social mammals. The second study examined whether living in a large group drove the need for complex numerical abilities (due to the need to keep track of large number of individuals, complex dyadic relationships, etc.) that have been seen in social mammals (including humans), and somewhat in birds including corvids. If so, the nutcrackers should not show the ability to comprehend numbers as well as more social animals that have been previously tested. On the other hand, if other evolutionary pressures drove the need for numerical abilities (i.e. the need to keep track of large numbers of stored food items), the food-hoarding nutcracker should demonstrate number competence on par or exceeding that of other animals tested so far. The last study directly examined the effect of group size on social intelligence. The need to keep track of a myriad of dynamic social relationships may have driven group-living animals to develop social intelligence (including behavioral flexibility in the presence of others). In that case, the nutcrackers should not show the same sensitivity to an observer as more social scrub jays that have been previously tested. On the other hand, if both scrub jays and nutcrackers faced evolutionary pressure to keep track of potential pilferers, social intelligence may have arisen as an adaptive specialization for guarding food resources in the corvid family of birds. If so, the asocial nutcracker should demonstrate cache-protection strategies (alter its behavior when it is observed by a conspecific), that are similar to those seen in the scrub jay. These three areas of cognition have also been selected because they not have been previously examined in nutcrackers, and would therefore contribute to the literature on cognitive abilities (other than spatial memory) in these birds.

CHAPTER II

TESTS OF INFERENTIAL REASONING BY EXCLUSION IN THE CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA)*

Abstract

I examined inferential reasoning by exclusion in the Clark's nutcracker (*Nucifraga columbiana*) using two-way object-choice procedures. While other, social corvids appear capable of engaging in inferential reasoning, it remained unclear if the relatively less social nutcracker is able to do so. In an initial experiment, food was hidden in one of two opaque containers. All of the birds immediately selected the baited container when shown only the empty container during testing. I subsequently examined the nutcrackers in two follow-up experiments using a task that may have been less likely to be solved by associative processes. The birds were trained that two distinctive objects were always found hidden in opaque containers that were always positioned at the same two locations. During testing, one of the two objects was found in a transparent 'trash bin', and was unavailable. The birds were required to infer that if one of the objects was in the "trash bin", then the other object should still be available in its hidden location. Five out of six birds were unable to make this inference, suggesting that associative mechanisms likely accounted for our earlier results. However, one bird consistently chose the object that was not seen in the "trash bin", demonstrating that nutcrackers may have the ability to use inferential reasoning by exclusion to solve inference tasks. These results suggest that the

evolutionary pressure of food-caching, rather than social organization, may have been an important factor in the ability of corvid birds to reason.

Introduction

Many cognitive scientists believe that the ability to reason is an important indicator of intelligence (Holyoak and Morrison 2005). Köhler (1925) described reasoning as involving "a mental reorganization of problem elements into a sudden solution". In one of Köhler's classical food gathering puzzles, chimpanzees (*Pan troglodytes*) were presented with bananas hanging above their reach. After a few unsuccessful attempts at obtaining the food, the chimps began to use tools such as boxes and poles in the enclosure to reach the food. To all appearances, the chimps were experimenting in their minds before manipulating the tools. The pattern of these behaviors would seem to involve insight and planning. Köhler suggested that insightful behavior allows an animal to bypass learning by trial and error. However, critics argue that insight is not fundamentally different from associative learning (Simonton 1999). Cognitive scientists have had considerable difficulty distinguishing between sudden insightful solutions and gradual development in performance due to associative learning. Although it is difficult to rule out associative explanations for insightful behavior (e.g., Simonton 1999), research suggests that animals may rely on processes that are more consistent with insight rather than learning.

A specific type of insightful problem solving, inferential reasoning by exclusion (also called exclusion performance or EP), has been defined as "selecting the correct alternative by logically excluding other potential alternatives" (Premack and Premack 1994). One way to study inferential reasoning by exclusion is to present a two-way

object-choice task, exposing subjects to either direct information (witnessing the hiding of a desired object) or indirect information (presenting an empty container), and providing them with sufficient but incomplete information to solve the problem (Erdöhegyi et al. 2007). To test this type of reasoning, Premack and Premack (1994) presented a problem with missing information to chimpanzees. They tested three chimps by placing a banana and an apple into two different boxes while a chimp watched. An experimenter then secretly removed the banana from the box, and ate the banana in full view of a chimp. The chimp was then given a choice between the two boxes. One of the three chimps immediately selected the other box as the one containing food (the apple). The Premacks concluded that the chimp likely inferred the location of food by reasoning: if the experimenter ate the banana, then the box that held the banana is now empty and therefore it should be excluded as a choice.

Likewise, Call (2004) used a simple two-way object-choice task to examine inferential capabilities in four primate species, chimpanzees, orangutans (*Pongo abelii*), gorillas (*Gorilla gorilla gorilla*), and bonobos (*Pan paniscus*). One of two containers was baited out of sight and then both containers were presented to an animal. In the *baited* condition, the contents of the baited cup were shown to the animals; in the *empty* condition, only the empty cup was shown; and in the *control* condition, the contents of neither cup were shown. Results from the *empty* condition indicate that all four species were able to choose the baited container, even when only the empty container was shown (often doing so on the very first trial). Since these primates were able to solve the problem immediately, Call suggested that the results are more consistent with reasoning than with a learning program. Likewise, in similar tests, several species of monkeys also

selected the baited cup when shown only the empty cup (i.e. capuchins, *Cebus apella,* Paukner et al. 2006; Sabbatini and Visalberghi 2008; Tonkean macaques, *Macaca tonkeans,* Petit et al. 2005; and baboons, *Papio hamadryas,* Schmitt and Fischer 2009). Indeed, many large social mammals seem to be able to use exclusion to solve various tasks (i.e. chimpanzees, Tomonaga 1993; Beran and Washburn 2002; bottlenose dolphins, *Tursiops truncatus,* Hermann et al. 1984; sea lions, *Zalophus californicus,* Schustermann and Kreiger 1984; Kastak and Schustermann 2002; dogs, *Canis familiaris,* Kaminski et al. 2004; Pilley and Reid 2011; and pigeons, *Columba livia,,* Aust et al. 2008).

While mammals have historically been examined for their ability to make logical inferences given their large brain size, cognitive abilities, and relative evolutionary proximity to humans, birds have been less well studied. However, recent advances in avian neuroanatomy suggest that both avian and mammalian forebrains are both derived from the pallium, an area that controls higher functions such as spatial reasoning and planning for the future (Jarvis and Consortium 2005). Correspondingly, much behavioral work with avian species, particularly corvids, over the past decade has indicated a greater degree of cognitive sophistication than was once expected, and suggests that the cognitive abilities of corvids are on par with mammals (for reviews see Emery and Clayton 2004; Emery 2006; Shettleworth 2010). For example, magpies (*Pica pica,* Pollok et al. 2000) Western scrub jays (*Aphelocoma californica*, Salwiczek et al. 2009) and Eurasian jays (*Garrulus glandarius,* Zucca et al. 2007) demonstrate an understanding of Piagetian object permanence. Scrub jays have been shown to have an episodic-like memory (e.g., Clayton and Dickenson 1998), and the ability to plan ahead for the future,

a trait which was previous viewed as uniquely human (Correia et al. 2007). New Caledonian crows (*Corvus moneduloides*) make and use tools, a skill that until recently was attributed only to chimpanzees and humans. They also exhibit meta-tool use (using a tool to get another tool), which suggests that they have an understanding of the purpose of the tools (Hunt and Gary 2004, Hunt et al. 2006). Corvids also demonstrate a wide variety of behaviors suggesting a high degree of social intelligence. For example, pinyon jays (*Gymnorhinus cyanocephalus)* use transitive inference to assess social relationships (Bond et al. 2003; Paz-y-Mino et al. 2004); and ravens (*Corvus corax*) are able to follow a conspecifics' gaze to locate food (Schloegl et al. 2007; Schloegl et al. 2008). Also, many species of corvids behave as if they are aware of another individual's knowledge; they protect their food by modifying various caching behaviors when they are observed by a conspecific. Examples include increased caching when observed (Eurasian jays, Bossema 1979), decreased caching (Northwestern crows, *Corvus caurinus*, James and Verbeek 1984; ravens, Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002; rooks, *Corvus frugilegus,* Simmons 1968; grey jays , *Perisoreus canadensis*, Burnell and Tomback 1985), alteration of cache spacing (magpies, Clarkson et al. 1986; grey jays, Waite and Reeve 1995), caching out-of-view (ravens, Bugnyar and Heinrich 2005; scrub jays, Dally et al. 2005 a and b) or in difficult-to-see locations (magpies, Clarkson et al. 1986; scrub jays, Dally et al. 2004), repeatedly moving caches when observed (Eurasian jay, Cramp and Perrins 1994; scrub jays, Dally et al. 2005 a and b), and privately moving caches that had been seen (Eurasian jays, Goodwin 1955; ravens, Heinrich and Pepper1998; scrub jays, Emery and Clayton 2001).

In light of the qualitatively similar cognitive processes between mammals and

corvid birds reported above, researchers have recently started to test for the ability of corvid species to make logical inferences. Using two-way object-choice procedures similar to Call (2004), Schloegl and colleagues (2009) found that ravens, a seed-caching corvid, were able to choose correctly using exclusion. In contrast, keas (*Nestor notabilis),* a large alpine parrot indigenous to New Zealand, were unable to do so. In a follow up study, jackdaws (*Corvus monedula),* a non-caching corvid, also did not demonstrate EP (Schloegl 2011). Carrion crows (*Corvus corone corone,* another seed-caching corvid) were subsequently tested using similar procedures (Mikolasch et al. 2011a). Although the carrion crows strongly preferred the cup that was last manipulated by an experimenter, in the absence of local enhancement some of the birds were able to make choices using an exclusion inference.

Two likely hypotheses for the evolution of cognitive abilities like inference by exclusion include the adaptive specialization hypothesis and the social intelligence hypothesis. The adaptive specialization hypothesis posits that species like corvid birds evolve specific cognitive abilities (e.g., tool use, cache protection, planning for the future) to adapt to problems in their socio-ecological environment (Kamil 1987; deKort and Clayton 2006). The ability of the corvids examined thus far to make an inference (ravens and carrion crows) also may arise through "adaptive specialization". Specifically, Mikolasch and colleagues (2011a) speculate that the adaptive specialization of caching food may lead seed-caching corvids to acquire the ability to infer. The finding that non-caching jackdaws fail to make a logical inference tends to support the adaptive specialization hypothesis. If this hypothesis holds true, then we can expect that other seed-caching corvids should also be able to use inferential reasoning.

Other factors besides specialized foraging abilities also might also contribute to the development of reasoning abilities, however. The "social intelligence hypothesis" (Byrne and Whiten 1988) posits that animals living in large groups acquire advanced cognitive abilities due to the pressures of living in a complex social network. The social intelligence hypothesis has been generally supported in primates, but less data are available for other groups (e.g., Ball 1998). According to the social intelligence hypothesis, social species would be more likely to make logical inferences, while solitary species would be less likely to do so. All the corvids tested thus far on inference by exclusion tasks have been highly social, so the social intelligence hypothesis has not been well explored in this regard. A wider sample of corvid species that differ with regards to traits like foraging strategy and social structure need to be examined to better understand which of these two ecological factors may be important for predicting advanced cognitive abilities such as making inferences.

Here I examined whether a member of the corvid family, the Clark's nutcracker (*Nucifraga columbiana*), can solve problems using inferential reasoning by exclusion. The Clark's nutcracker is a seed-caching corvid that is closely related to crows and jackdaws (Ericson et al. 2005; Ekman and Ericson 2006; deKort and Clayton 2006), which have been examined for their ability to make a logical inference. Like these other corvids, nutcrackers have had a strong selective pressure to cache food for survival. Unlike these other corvids, however, the nutcracker is a specialist that depends largely on the seeds of one species of pine tree (Lanner 1996). Nutcrackers also differ in that they are also one of the least social corvids, as they do not live in large flocks or nest cooperatively (Balda et al. 1996). I used a two-way object-choice task similar to that

employed by Call (2004) and Premack and Premack (1994) to examining inferential reasoning in Clark's nutcrackers. If foraging behavior (caching) contributes to the evolution of cognitive attributes such as making a logical inference, the nutcrackers should perform comparably to ravens and carrion crows on inference tasks. In contrast, if social factors play more of a role in the development of cognitive processes like making an inference, then nutcrackers should be less comparable to these birds, given that they are less social.

Experiment 1

Four nutcrackers were tested using a two-way object-choice task similar to that used by Call (2004). I initially trained the birds that only one of two opaque cups with removable covers contained food. Next, I administered tests in which the birds were given partial information (revealed the contents of either the baited or the empty cup) or no information (shown the contents of neither cup). Correct choices early during the partial information conditions may indicate an ability to infer by exclusion that has been shown in similar work with mammals (bottlenose dolphins, *Tursiops truncatus,* Hermann et al 1984; sea lions, *Zalophus californicus,* Schustermann and Kreiger 1984; Kastak and Schustermann 2002; dogs, *Canis familiaris,* Kaminski et al. 2004; Pilley and Reid 2011; monkeys, Paukner et al. 2006; Sabbatini and Visalberghi 2008; Petit et al. 2005; Schmitt and Fischer 2009; apes, Tomonaga 1993; Beran and Washburn 2002; Call 2004) and other social corvids that cache food (Schloegl et al. 2009; Mikolasch et al. 2011).

Methods

Animals. Adult nutcrackers were trapped in western North America, and housed at the University of New Hampshire. The birds were of undetermined sex and had

previously been used in several tests of spatial orientation and navigation (Gibson and Kamil 2001; Gibson and Kamil 2005) and the ability to use human gestures to locate food (Tornick et al. 2011). The birds were kept in individual cages in an environmentally controlled room (22° C, 14:10h light: dark cycle). Birds were maintained at 90% of their free-feeding weight, by regulating intake of turkey starter, pigeon pellets, striped sunflower seeds, and mealworms following experimental sessions. The birds had unlimited access to grit and water.

Apparatus. The nutcrackers were individually trained and tested in a white melamine experimental chamber measuring 45 cm wide x 45 cm long x 60 cm high (Figure 1). A single perch sat 5 cm above the floor in the center of the chamber. The front of the chamber was a clear Plexiglas® panel with two holes near the base of the apparatus (one left and one right) measuring 5 cm in diameter. Through these two holes, the birds could access two identical opaque 5 cm diameter x 4 cm high cylindrical PVC food cups with pivoting lids. A tray with two 4.75 cm diameter holes (one left and one right) was fitted to hold the two food cups, and was positioned in front of the chamber. The experimenter could move the tray forward in a track, bringing both the food cups within reach of the birds. After a bird selected one of the cups by opening it, the experimenter quickly slid the whole food tray away, so that only one choice could be made per trial. Background white noise was projected into the room through an overhead speaker. An overhead Microsoft VX-6000 LifeCam video camera was used to view a bird's choice during each session via a Dell Inspiron 6400 laptop computer.

Pre-training. The birds were taught to open the lids to the cups with their beaks in their home cages. Next, to acclimatize the birds to the experimental apparatus each bird

was housed individually in the chamber for a one-hour daily session for five consecutive days. Training commenced once the birds were readily opening cups and familiarized with the apparatus.

Training. During each trial, a bird was placed in the chamber and a single pine nut (a favorite food) was first shown to a bird for three seconds. Two cups were always used: one of the cups contained food (pine nuts) and the other cup remained empty. A styrofoam partition (60 cm wide x 45 cm high x 5 cm deep) was used as a visual barrier to prevent the birds from seeing the experimenter bait one of the food cups. The experimenter placed several pine seeds randomly into one of the two identical cups out of sight behind the partition. The partition was then removed and the cups were placed into the sliding tray and moved toward the birds, yet just beyond their reach. The left cup was opened for three seconds and then closed. The right cup was then opened and closed so that the bird had seen the contents of both cups. Next, the tray holding the cups was pushed forward towards the holes in the Plexiglas®, and an opaque curtain between the birds and the experimenter was closed so that the birds could not see the experimenter during the choice phase. The birds were required to choose a food cup by approaching one of the holes in the Plexiglas® and opening the pivoting lid with its beak. The bird had to remember which cup held the food, and select that cup. If a correct choice was made, the bird received food reinforcement (a pine nut). If an incorrect choice was made, the tray was slid back and the bird received no food and a ten second time-out with the house lamp turned off. The position of the cup containing the food (the baited cup) was pseudo-randomized between the left and right positions in the sliding tray, with no more than two trials on the same side consecutively, and the number of times per side balanced

for each session. Also, the location of the food was pseudo-randomized between the two cups to ensure that the birds could not use any slight differences in the cups as a cue. Birds were given one session per day consisting of eight training trials. If a bird did not make a choice within 30 seconds, the trial was repeated. If the bird did not make a choice for three trials in a row, the session was ended. The criteria required to begin testing was seven out of eight correct choices for five consecutive days. Training lasted for a mean of 13.2 (range = 12-15) days.

Testing. I examined the birds in the following three test conditions: 1) *baited*- birds were only shown the contents of the cup containing food, 2) *empty*- birds were only shown the contents of the empty cup (see video 1), and 3) *no information/control* - birds were not shown the contents of either cup. The purpose of the control condition was to eliminate the possibility of the birds using odor cues or inadvertent cues from the experimenter. Each bird encountered daily sessions of eight trials. Seven of these eight trials were the same as the training condition (the contents of both cups were shown). One of the eight trials was one of the three test conditions, randomized between the third and sixth trials. Each bird was tested a total of 16 times in each of the three conditions. Two birds (Susan and Fitz) encountered all 16 of the *empty* condition trials, then all 16 of the *baited* trials, and then all 16 of the *control* trials in sequence during testing. Two other birds (Starr and Betsy) encountered 16 trials in each of the three conditions in random order, with the exception that no more than two consecutive sessions repeated the same condition.

Analysis. The dependent variable was the bird's choice (correct or incorrect). I pooled the data from all four birds and used Fisher exact tests to compare the following

pairs of conditions: *empty* versus *baited*, *empty* versus *control*, and *baited* versus *control* (see Call 2004). I also conducted a second set of analyses that focused on individual choices. For each bird the number of correct choices out of 16 for the *empty*, *baited*, and *control* conditions was compared to chance performance (8 of 16) using binomial tests (Call 2004; Tornick et al. 2011). Family-wise type I error rate was controlled using a step-down Holm-Bonferroni procedure (Holm 1979; Ludbrook 1998). Adjusted alphas (α_{obt}) are reported and all tests were two-tailed.

Results and Discussion

Collectively, the nutcrackers made more correct choices in both the *Baited* (Fisher exact test, $P < 0.001$) and *Empty* conditions ($P < 0.001$) than they did in the *Control* condition and there was no difference in the number of correct choices between the *Empty* and *Baited* conditions ($P = 0.157$) (Figure 2). Susan chose the correct cup in the *Empty* condition in 14 out of 16 sessions, and chose correctly for the first eight consecutive sessions before making an incorrect choice (Figure 3). Susan's performance was significantly better than chance across the 16 sessions in the *Empty* condition (87.5%, $\alpha_{obt} = 0.020$, binomial test, $P = 0.002$). In the *Baited* condition, Susan also chose the correct cup significantly more often than chance (93.75%, $\alpha_{obt} = 0.033$, $P = 0.002$). In the *Control* condition, Susan's performance was not significantly different than chance (50%, $\alpha_{obt} = 0.025$, $P = 0.196$). Starr also made more correct choices in the *Empty* and *Baited* conditions than the *Control* condition (Figure 3). Notably, Starr chose correctly in all 16 sessions (Figure 3). In the *Empty* condition, Starr's performance was significantly better than chance (100%, $\alpha_{obt} = 0.002$, $P < 0.001$). In the *Baited* condition, Starr also chose the correct cup significantly more often than chance (93.75%, $\alpha_{obt} = 0.013$, $P <$

0.001), but not in the *Control* condition (43.75%, $\alpha_{obt} = 0.013$, $P = 0.175$). Betsy too, made more correct choices in the *Empty* and *Baited* conditions than the *Control* condition (Figure 2). Betsy chose correctly in 14 out of the 16 sessions (Figure 3). Betsy's performance was significantly better than chance in the *Empty* (87.5%, $\alpha_{obt} = 0.020$, $P = 0.002$), and *Baited* conditions (93.75%, $\alpha_{obt} = 0.017$, $P < 0.001$), but was not significant in the *Control* condition (50%, $\alpha_{obt} = 0.025$, $P = 0.196$). Fitz also made more correct choices in the *Empty* and *Baited* conditions than the *Control* condition (Figure 2). Fitz chose the correct cup in the first seven sessions; however, after the first several sessions Fitz's performance declined (12 correct choices overall out of 16), perhaps due to a lack of motivation (Figure 3). However binomial tests indicated that, in Fitz's performance was still significantly better than chance in the *Empty* (75%, $\alpha_{obt} = 0.050$, P = 0.028), and *Baited* (81.25%, $\alpha_{obt} = 0.033$, $P = 0.009$) conditions, but not significantly different than chance in the *Control* condition (50%, $\alpha_{obt} = 0.025$, $P = 0.196$).

A goal of Experiment 1 was to compare the ability of the relatively asocial Clark's nutcracker to make logical inferences with that of more social corvids (food-caching ravens and carrion crows, and non-caching jackdaws) that have been examined previously in comparable inference tests. When the contents of only the empty cup were shown, all four nutcrackers were able to successfully choose the correct ("other") cup. Correct choices during the novel partial information test period also occurred early indicating that the nutcrackers had not learned a correct response pattern during testing. Thus, the nutcrackers' performance is comparable to the performance of related, but highly social corvids (ravens, Schloegl et al. 2009; carrion crows, Mikolasch et al. 2011a) in this test of inferential reasoning. Notably, non-caching jackdaws failed to solve a

similar two-way object task of logical reasoning (Schloegl 2011). Combined, the results suggest that food-caching in corvids may be a better predictor of the ability to make a logical inference than is social organization.

However some critics (i.e. Aust et al. 2008) have argued that simpler associative mechanisms, rather than reasoning, may account for the ability of animals to correctly solve the two-choice inference task. Animals given these tests may rapidly learn or are predisposed to avoid an empty cup. Likewise, local enhancement of cues near the correct cup may also play a role. Carrion crows prefer a cup that was last manipulated by an experimenter (Mikolasch et al. 2011a). Therefore, in Experiment 2, I examined the ability of nutcrackers to again make an inference-by-exclusion using a task that may be more difficult to solve quickly using associative mechanisms.

Experiment 2

In Experiment 2, I presented the birds with a task comparable to that used by Premack and Premack (1994). I first trained the birds that pine nuts were available always in a fixed location (a cup on the left side of the apparatus), and mealworms were available always in a second location (right cup). They simultaneously learned that food was unavailable when it was found in a clear glass beaker (the "trash can"), located in the center of the sliding tray in front of the apparatus. During the critical test, the two closed choice cups and the trash can were positioned in front of the nutcracker outside the apparatus. One type of food (e.g., pine nuts) was hidden at its learned location (left cup), and the other type of food (e.g., worms) was visible and unavailable in the trash can. Nutcrackers made a correct choice during this test if they correctly identified the type of food in the trash can and subsequently choose the other (available) food type hidden in

the learned location.

Methods

Animals. Seven Clark's nutcrackers, including the four nutcrackers from Experiment 1, plus three additional nutcrackers with a similar experimental history to those used in Experiment 1 were used in Experiment 2. The birds were maintained as in Experiment 1.

Apparatus. I conducted Experiment 2 in the same apparatus that was used in Experiment 1, except that I added a trash can, a clear beaker that was 6 x 10 cm centered between the position of the left and right cups on the sliding tray. Any food in the trash can could be seen by the birds but was not accessible.

Food Preference Pre-test. I initially examined whether each bird had a food preference for either mealworms or pine nuts. I presented the birds with one pine nut and one mealworm separated by a distance of 20cm on the floor of their home cage. The food item that they first picked up with their beak was deemed the more preferred of the two items. Preference testing occurred once a day prior to daily feeding for a total of twenty days.

Training. During the first 6 of 18 trials of a daily session, I trained the birds that food that was placed in a trash can was unavailable. During these six trials I baited the two cups (in full view of the birds) with a small piece of a peanut left inside part of a peanut shell using the procedures described in Experiment 1. I moved the sliding tray with the cups and the trash can toward the front of the apparatus, but out of reach of the nutcracker. I then raised the opaque visual barrier between the subject and the tray for 3s. Next, I removed the barrier and, within view of the bird, extracted the peanut from either

the left or the right cup and simultaneously activated a bell to indicate one of the items had been taken from a cup. The piece of peanut was held for 3s in the center of the front wall of the apparatus approximately 5cm above the trash can and until the bird appeared to make visual contact with the food. I then dropped the peanut into the trash can to render it inaccessible. The bird was then allowed to open either the left or right cup. The side/cup from which the nut was removed was randomized across trials with no more than two consecutive trials on the same side. The side in which I removed the nut also was counterbalanced across trials. If the nutcracker made a correct choice it was allowed to eat the peanut. If the bird made an incorrect choice (chose the same cup from which the nut had been removed) the tray was slid away and the bird was not allowed to make a second choice. Following an incorrect choice I indicated the correct location to the bird by opening the lid and tipping the cup to reveal the contents for 3s. Correction trials were given following incorrect choices. After each trial, the opaque white curtains were closed and the unused shells and nuts were removed. Nutcrackers were required to make 5 of 6 correct responses for a minimum of two consecutive days to continue on to testing. After 7-13 days (mean = 9.2 days, SD = 2.2) all of the birds reached this criteria, however training continued until all of the birds simultaneously completed 30 days of food-place training (see below).

Food-place Training. The final 12 trials of the daily session were devoted to training the birds that a pine nut was located on the left side of the apparatus (the subject's right side) in a black and white dotted cup, and a mealworm was located on the right side of the apparatus (the subject's left) in an orange and white striped cup. These visually distinctive cups served to facilitate learning of the fixed food locations. The trash

can (though not used during this phase of training) was placed in the center of the sliding tray.

The experimenter showed either a pine nut or a worm to the nutcracker for a minimum of 3s and until it appeared that the nutcracker had made visual contact with the food item. I positioned the sliding tray close enough for the birds to see, but not access, the cups. Out of sight of the bird, the experimenter then baited either the left cup with a pine nut, or the right cup with a mealworm, using baiting procedures described previously. Across the 12 trails, whether a pine nut or worm was presented was balanced and pseudo-randomized, with the exception that there were no more than two consecutive trials using either food. Next, I moved the tray forward and the subject was allowed to investigate the cups for 3 min, and eat the food item found inside. After the bird had explored the cups, the food tray was retracted for a two minute delay. Food-place training continued for 30 days so that the birds could learn the location of each food type.

Testing. Each daily session of testing consisted of two trials. The first type of trial was the inference test. During this type of trial I positioned the tray containing the two cups and trash can away from the apparatus and baited the left (black and white dotted) cup with ½ pine nut. I then baited the right (orange and white striped) cup with a small mealworm. The tray was moved half-way forward, but still out of reach of the subject. The opaque barrier was placed between the subject and the cups and the experimenter removed either the ½ pine nut from the left, black and white dotted cup or the worm from the right orange and white stripped cup. Both cups were opened and closed using the procedures described previously. The bell also was rung to indicate that food and been extracted by the experimenter from one of the two cups. The type of food that was

removed was randomized across trials with the constraint that the same food item could not be removed for more than two consecutive trials. Next the opaque barrier was removed and the experimenter held the food that had been extracted in the center of the Plexiglas wall of the apparatus for 3s and until the bird appeared to have seen it. The food item then was dropped into the clear trash can and the lid placed on top while the subject appeared to be watching. The tray was moved forward and the bird was allowed to open one of the two cups. To make a correct choice, a bird was required to choose the cup that was associated with the food that was not currently in the trash can. A bird made an incorrect choice when it chose the cup that had contained the food type that was currently in the trash can. Following an incorrect choice, the contents of the unchosen cup were revealed to the bird, and then the tray was moved away from the apparatus.

I also ran a control test (second type of trial) to rule out the possibility that the experimenter was providing unwanted cues or that the birds were using odor as a cue to make their choices. During these trials the experimenter baited the left and right cups (note: different cup sleeves were used for these control trials) with peanuts in view, but out of reach of the nutcracker. Next, the opaque barrier was placed between the bird and the tray. Out of sight of the bird, the experimenter then removed one of the peanuts from either the left or right cup and rang the bell. Next, I removed the barrier and while the subject watched, the peanut was placed into the trash can between the two cups on the tray and the subject was allowed to make a choice between either the left or right cup. If the bird made an incorrect choice it found nothing. The bird was allowed to see inside the empty cup then the experimenter quickly slid the tray away so that it could not extract the other peanut. The bird was shown the remaining peanut by tipping the cup and opening

the lid (non-reward). One control and one inference test was presented to the birds in random order each day for ten consecutive days.

Food preference post-test. To see if any individual bird's food preference had changed over the course of the experiment I repeated the food preference tests at the conclusion of testing. The procedures were identical to those described previously.

Analysis. I pooled the data from all seven birds and ran binomial probability tests on the number of correct choices for both the inference tests and the control tests. I used Fisher exact test to compare the results from the inference test and control tests. Individual performance was also analyzed. For each individual bird, the number of correct choices (out of a total of ten) was compared to chance performance using binomial tests. To test for a side or food bias, the side chosen (left or right, number of choice out of 10) and type of food (pine nut or mealworm) were also compared using binomial probability tests. For these individual analyses, family-wise type I error rate was controlled using a step-down Holm-Bonferroni procedure, and adjusted alphas (α_{obt}) are reported, as in Experiment 1. I analyzed each bird's potential preference for either the worms or pine nuts (both before and after testing) using binomial probability tests, as described in Experiment 1.

Results and Discussion

Food preference. At the time of the pre-test, six of the seven birds preferred pine nuts over mealworms. Susan and Fitz chose 17 out of 20 pine nuts (binomial tests, α_{obt} = 0.033, P = 0.001), Sony chose 15 out of 20 pine nuts (α_{obt} = 0.017, P = 0.015), Starr, Artz and Puck chose 14 out of 20 (α_{obt} = 0.0009, P = 0.037). Only Betsy preferred mealworms (14 out of 20, α_{obt} = 0.0009, P = 0.037). An analysis of the food preferences after the test

indicated that the food type that each bird preferred during the pre-test did not change over the course of the experiment.

Inference tests. Collectively, during the inference tests, the birds did not choose the correct cup (the cup that contained the food type not seen in the trash can) more often than would be expected by chance (35 correct out of 70, binomial test, $P = 0.095$). They also choose either cup with equal probability during the control tests (38 correct out of 70, $P = 0.074$). There was no reliable difference in number of correct choice between the inference and control tests (Fisher exact test, $P = 0.096$). Likewise, my analysis of the choices made by the individual birds revealed a similar trend, as none of the birds chose the correct cup (the food type not seen in the trash can) more often than the incorrect cup during the inference tests (Figure 4). Susan made 6 correct out of 10 correct choices (binomial tests, $\alpha_{obt} = 0.02$, $P = 0.205$). Betsy, Artz, and Puck made 5 correct out of 10 correct choices ($\alpha_{obt} = 0.008$, $Ps = 0.246$)and Starr and Fitz made 4 correct choices out of 10 ($\alpha_{obt} = 0.02$, $Ps = 0.205$).

A proportion of the errors made during testing could be attributed to the fact that the birds had a strong preference to choose the cup that contained their most preferred food, regardless of which item was in the trash can. Susan, Starr, Artz and Puck chose the cup that contained the pine nuts on 10 out of 10 trials ($\alpha_{obt} = 0.02$, $Ps = 0.0009$); Fitz and Sony chose the cup with the pine nuts 9 out of 10 inference test trials ($\alpha_{obt} = 0.009$, $Ps = 0.009$). Likewise, Betsy (the only bird that preferred mealworms in the food preference pre-test) favored the cup with mealworms in the inference test, regardless of which food type was in the trash can (10 out of 10, $\alpha_{obt} = 0.02$, $P = 0.0009$).

During the control test trials none of the birds located the peanut better than

would be expected by chance. Susan, Sony, and Puck found the peanut on 7 out of 10 trials (binomial tests, $\alpha_{obt} = 0.02$, $Ps = 0.117$). Starr and Artz found the peanut during 5 out of 10 trials ($\alpha_{obt} = 0.008$, $Ps = 0.246$), Betsy during 4 out of 10 trials ($\alpha_{obt} = 0.01$, $P = 0.205$); and Fitz during 3of 10 trials ($\alpha_{obt} = 0.02$, $P = 0.117$). These results suggest that the birds were not able to use odor or experimenter-given cues to solve the problem. Rather, due to the potential ambiguity of the control tests the birds primarily selected the cup/side that was consistent with their food preference. Starr made 10 out of 10 choices to the left (pine nut) cup ($\alpha_{obt} = 0.05$, $P = 0.0009$); Artz made 9 such choices ($\alpha_{obt} = 0.02$, $P = 0.009$) and Susan, Sony and Puck chose the left cup on 8 of 10 occasions ($\alpha_{obt} = 0.01$, $Ps = 0.009$); Fitz made 6 choices to the left cup ($\alpha_{obt} = 0.007$, $P = 0.205$). Likewise, Betsy made 9 of 10 choices to the right cup, which had contained worms during training ($\alpha_{obt} = 0.02$, $P = 0.009$).

Perhaps, because the birds had never seen either worms or nuts in the trash can before, the conditions of the test became ambiguous and the birds resorted to choosing the cup that was associated with their more preferred food item. Previous work has shown that it is sometimes difficult for food-deprived animals to inhibit responses toward their preferred food (human children, Mischel et al. 1989; chimpanzees, Boysen and Berntson1995; humans, pigeons and rats *Rattus norvegicus*, Tobin and Logue 1994). In this experiment, the birds appeared to have a strong bias to go to the cup that was associated with their most preferred food, even if it was not available during a trial. Therefore, to eliminate the possibility that food preferences could be preventing the birds from demonstrating the use of inferential reasoning, I conducted a third experiment.

Experiment 3

In this experiment, the birds would now be required to make an inference about the location of a non-food object. I used procedures that I developed in Experiment 2; however, to eliminate the problems previously caused by food preference biases, I replaced the two types of food used in Experiment 2 (pine nuts and worms) with two equivalent toys (ball and dolphin).

Methods

Animals. Six of the seven Clark's nutcrackers that were used in Experiment 2 were used in Experiment 3. One bird was excluded because of health related issues.

Apparatus. I used the same apparatus that had been used in the previous experiment. I made a few minor modifications to the apparatus. I created an additional choice hole in the center of the Plexiglas® wall in the front of the chamber, and added a .65 cm diameter clear plastic tube that was positioned at the top of the outside of the apparatus and went through an exterior wall into the apparatus. I used the tube to deliver pine nuts onto the floor near the front center of the apparatus. I also replaced the trash can used in Experiment 2 with a shorter one (6cm x 6 cm) that had a tightly fitting removable lid.

Toy Familiarization and Tube Acclimatization. This training took place in the birds' home cage. The birds were presented with two novel objects, a plastic yellow porcupine ball (2.5 cm in diameter) and a blue and white plastic dolphin toy (2 x 2 x 3 cm). The birds were required to lift the object in the air with their beaks, and were reinforced with half of a pine nut for doing so. The presentation of the toys alternated so that the birds experienced an equal number of exposures to the ball and dolphin per day. Simultaneously, the birds were re-acclimated to the experimental test chamber with the

new food-delivery tube. I dropped a half of a pine nut down the clear plastic tube and into the front center of chamber and the bird was allowed to retrieve it. Familiarization lasted one to two weeks until all the birds were reliably manipulating both objects and retrieving food from the tube in the apparatus.

Toy Preference Pre-test. I conducted preference tests as in Experiment 2, except that the two food items were replaced with the two toys. I recorded which toy the bird touched first for 18 days. Preference tests were also administered after testing, as described below.

Trash Can Training. I initially trained the birds to open one of the opaque cups used in Experiment 2 that had one of the two toys inside (randomly determined). Training was conducted in their home cage and the birds were reinforced with a pine nut for opening the cup and picking up the toy inside. Next, I presented the birds with two additional different types of training trials in their home cage. These trials were interspersed with maintenance trials (as described above) in which the birds open the lid to extract a toy for reinforcement. During one of these two types of trials one of the toys (randomly determined) was placed in the trash can without the lid and the bird could extract the toy for reinforcement. During the other type of training trial I put one of the toys inside the trash can and then the lid was placed on top. I left the trash can in the cage for 30s and recorded the number of pecks the bird made to the trash can or lid. I expected the number of pecks to the lid to decrease over time as the birds learned about the inaccessibility of food when the lid was on. The birds encountered each of the three types of training trials four times in each daily session, for a total of 12 trials. The order of the trials was randomized with the constraint that no more than two trials of any type

occurred in a row. After a mean of 28.83 days (SD = 2.79) pecking at the trash can/lid appeared to reach asymptote (mean number of pecks at the beginning of training = 85.29 pecks, SD = 39.73, mean number of pecks at the end of training = 14.19 pecks, SD = 14.05), and testing began.

Toy-place Training. The procedures were identical to those of the food-place training in Experiment 2 except that toys replaced the two types of food. I trained the birds that the ball was always located on the left side of the apparatus and the dolphin was always located on the right side. When a subject opened one of the opaque cups and manipulated the toy inside, a ½ pine nut was delivered down the clear tube.

Testing. The procedures for the inference tests were similar to those used for Experiment 2 except that two toys were used instead of the two food types, and correct choices (opening the cup that contained the toy not seen in the trash can) resulted in the delivery of a ½ pine nut into the chamber via the plastic tube (see video 2). Each bird received one inference and one control test per day for 10 days.

Analysis. Each bird's toy preference (ball or dolphin, before and after testing) was analyzed individually using binomial probability tests, as in Experiment 2. I analyzed the pooled and individual choices during testing as described in Experiment 2.

Results and Discussion

Toy Preference. None of the birds demonstrated a preference for either the ball or the dolphin prior to testing. Five of the six birds touched the ball first 8 out of 18 times ($\alpha_{obt} = 0.017$, $Ps = 0.167$). Starr touched the ball first 9 out of 18 times ($\alpha_{obt} = 0.008$, $P = 0.185$). The birds continued to fail to display a preference for either toy after testing (all $ps > 0.05$).

Inference Test. Analysis of the choices made by all of the birds revealed that they did not choose the correct cup more than would be expected by chance (62 correct out of 120 choices, binomial test, $P = 0.068$). However, an analysis of the bird's individual choices revealed that Starr correctly chose the cup that contained the toy that was not in the trash can during 17 of 20 trials (binomial test, $\alpha_{obt} = 0.009$, $P = 0.001$, Figure 5). The other five birds did not make more correct choices than would be expected by chance. Sony made 11 of 20 ($\alpha_{obt} = 0.011$, $P = 0.160$), Betsy, Artz, and Puck made 9 of 20 ($\alpha_{obt} = 0.011$, $Ps = 0.160$), and Susan made 7 out of 20 correct choices during the inference test ($\alpha_{obt} = 0.025$, $P = 0.074$). In contrast to Experiment 2, only one of the six birds demonstrated a side bias (chose the cup containing the dolphin on the right) more than would be expected by chance (Artz 85%, $\alpha_{obt} = 0.009$, $P = 0.001$).

In this experiment, I attempted to eliminate the difficulties that occurred when two unequally favored foods were presented (Experiment 2). The pre-and post- toy preference tests indicate that the birds did not have a strong preference for choosing one of the toys (sides) over the other. However, even with this bias eliminated, only one of the six subjects was able to consistently make the correct inference about the location of the remaining toy. It would appear that my inference task was a difficult problem for the nutcrackers to solve, given the failure of all the birds to solve the task in Experiment 2 and most of these same birds to do so in Experiment 3. Despite this fact, one bird (Starr) seemed to use inferential reasoning to solve the problem. Starr's behavior during the choice phase of each test may account for his ability to solve the problem. During each trial Starr moved in front of the trash bin and looked at the contents before making a

choice. The other birds did not appear to consistently exhibit this behavior. These issues will be discussed further in the General Discussion below.

General Discussion

Several features of the environment of the Clark's nutcrackers make them well suited for comparative investigations of intelligence, such as the ability to make a logical inference, in corvid birds. Unlike many other corvids, nutcrackers inhabit high pine forests and are specialist foragers, depending largely on the seeds of one species of pine (*Pinus edulis*) for their survival (Lanner 1996). Tens of thousands of these seeds are stored in the autumn; then are recovered over the winter as food for survival (Balda and Kamil 2006). This remarkable ability has made nutcrackers a textbook model of spatial cognition in animals. Likewise, while most corvids live in social groups and flock or nest cooperatively, nutcrackers are believed to be far less social than many other caching and non-caching corvids (Balda et al. 1996). Thus, I was interested in comparing the performance of nutcrackers with other corvid birds that have evolved in different social and physical environments to examine how a number of cognitive abilities may have evolved for this group of birds.

I used the two-way object-choice procedure described by Call (2004) and employed by others to test inferential reasoning in Experiment 1. Two cups were baited out of sight and then either the baited or empty cup was shown to the birds. When the birds were shown only the contents of the empty cup (inference test), all of the nutcrackers immediately chose the baited cup. The performance of the nutcrackers on this task is similar to that of two other seed-caching corvids, ravens and carrion crows given comparable tasks. Schloegl and colleagues (2009) examined exclusion performance in

ravens and keas using a two-way object-choice task with food hidden in one of two bowls. Food was baited out of sight, and then an experimenter lifted either the baited or the empty bowl (or neither), to reveal the contents underneath. When only the empty bowl was lifted, the ravens (like the nutcrackers in the current study) but not the keas, were able to choose the baited bowl. These authors also tested both species in another task in which the birds were required to search for food in two differently shaped PVC tubes. There were several conditions in which the tubes were either straight or bent, and the food was either visible or out of view. Thus, they gave the birds partial information to make an inference about the content of the two tubes. Again, the ravens were more successful then the keas. In a follow up study (Schloegl 2011), non-caching jackdaws were tested with the same set of tasks. In contrast to the ravens, the jackdaws demonstrated very limited evidence of exclusion abilities, choosing at chance when they could not see the food. However another caching corvid, the carrion crow, was tested with the same procedure; many of the birds were able to choose by exclusion (Mikolasch et al 2011a).

There are several possible explanations for the results of the current (and previous) studies. The subjects could have reasoned, "cup A is empty; therefore it should be excluded as a choice". Simpler associative mechanisms could also account for the results, however. One type of associative mechanism, local enhancement (i.e. tendency to search in the last place an experimenter touched), can sometimes influence animals' choices in these types of problems. Several past experimental paradigms examined the use of local enhancement to solve two-way object-choice tasks. Dogs seem to prefer to use human-generated cues to find food, but can also solve simple EP tasks in the absence

of such cues (Bräuer et al. 2006, Erdöhegyi et al. 2007). Mikolasch and colleagues (2011a) also found that carrion crows prefer a cup that was last manipulated by an experimenter. However, in my experiments local enhancement was less likely because the cups were baited out of view of the subjects. Alternatively, in the current study and many of the others mentioned above, the birds may have learned to avoid the empty cup (S-) during training since it was never paired with food. During testing with the empty cup condition, the birds may have made a learned response to the alternative cup after encountering the empty one. Indeed, in previous tests of EP animals such as apes (i.e. Call 2004) may also have used simple associative mechanisms (see Aust et al. 2008) to solve inference problems. The fact that nutcrackers (and the other corvids tested on this paradigm) acquired the task rapidly and also performed at a high level early during testing may suggest that something more than associative learning was involved, however.

In Experiments 2 and 3, I used procedures developed by Premack and Premack (1994) as an additional test of inferential reasoning. In these experiments, I tried to reduce the probability that learning history (such as avoiding an empty cup) could account for the success on the inference test. Specifically, the birds had to recognize that the item in the trash can was unavailable and select the alternative object in its learned location/cup. In both Experiments 2 and 3 most of the nutcrackers failed to solve the inference test and selected between the correct and incorrect cup at chance. In Experiment 2, the ambiguity of the inference test likely resulted in all of the birds selecting the cup that had been paired with their favorite food, regardless of which food was seen in the trash can. When the potential for a food preference was eliminated during

the inference test in Experiment 3, the nutcrackers still largely failed to make the correct choice. Notably however, one bird (Starr) successfully solved the problem in Experiment 3. So are nutcrackers capable of making an inference by exclusion?

The results from Experiment 1 are largely consistent with other tests of EP with other caching corvids; that is, after being shown and empty cup they select an alternative cup that contains food. While the nature of the mechanisms that account for this performance may be debated, the fact that seed caching nutcrackers performed similarly to other seed caching corvids suggests a strong role for caching as a selective pressure for such behavior (see below). Compared to Experiment 1, the gap between what was learned during training and the ability of the birds to use that learned information to directly solve the inference test in Experiments 2 and 3 was quite large making the inference test more challenging for these later experiments. As pointed out above, one bird (Starr) was able to solve the inference task in Experiment 3. My informal observations of Starr's behavior throughout testing indicated that it was much more attentive to the critical features of the task in Experiment 3 (e.g., trash can). Based on the gap between the training given in Experiment 3 and the inference test it would seem like Starr had attended to the critical feature of the problem and made an inference about where food was located. Thus, it would appear that the results from one bird indicate a relatively impressive ability to make a logical inference. Perhaps, the other nutcrackers failed to attend to the critical features of the task because they had not learned the role of the trash can or failed to attend to the identity of the item in the trash can (though the results from training would suggest otherwise). One important implication of the results from all three experiments is that animals may be capable of using multiple mechanisms

to solve problems of inference by exclusion. Indeed, the failure of many nutcrackers to solve the inference test during Experiment 3 may have been because the birds were trying to use associative mechanisms that may have been largely successful earlier in the study.

If I accept the demonstration that one nutcracker is capable of a fairly sophisticated inference and that the other nutcrackers performed comparably to other seed caching corvids then I may be able to speculate about why this ability may have evolved for seed caching corvids more broadly. Mikolasch and colleagues (2011b) have suggested that EP may have evolved as an adaptive specialization (Kamil 1987; Shettleworth and Hampton 1998; deKort and Clayton 2006) to the pressures of caching and recovering food. Such an explanation would account for why caching corvids generally succeed, but non-caching corvids generally fail on inference tests tasks. Non-caching species like jackdaws (and also keas, Schloegl et al. 2009) may not pay close attention to food location or to the absence or presence of food; a trait which may have led to inferential reasoning abilities in caching species (Mikolasch et al. 2011). Gould-Beierle (2000) suggests that non-caching species may be more likely than caching species to return to an empty cache site to see if food had been replenished. Thus, caching species may be predisposed to knowing more about an "empty" site.

Another factor that might influence the development of complex cognition in a species is sociality, because the pressures of living in a large group might drive the need for complex problem-solving skills. The results of this study, however, do not support the social intelligence hypothesis. Even though nutcrackers are far less social than other corvids, in Experiment 1 their performance is on par with more social corvids like ravens. This may be the case because, although nutcrackers are less social, they need to be aware

of complex social interactions related to caching because they are still subject to pilfering by conspecifics, just as are ravens (Bugnyar and Kotrschal 2002). For the nutcracker though, because it inhabits such a harsh environment, being aware of potential pilferers may be extremely important for survival. It will be important to closely replicate this study using more social corvids to see if the majority of individuals excel compared to nutcrackers on the more complex inference task. My preliminary findings suggest, at least with the tasks tested here, that other factors (like foraging strategy or genetic relatedness) may be more important than sociality. It may also the case that several of these hypotheses work concurrently to shape cognitive abilities like EP (Rifkin 2007). Additional cognitive tests of the asocial Clark's nutcracker also will be extremely useful in further examining the social intelligence hypothesis. Like the more social corvids, the nutcracker may be capable of other higher cognitive processes, such as the use of human-generated cues (Tornick et al. 2011), social cache-protection behavior (Clary and Kelly 2011), and inferential reasoning (this study).

CHAPTER III

AN INVESTIGATION OF NUMERICAL DISCRIMINATION BY THE CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA*)

Abstract

I examined number discrimination in the Clark's nutcracker (*Nucifraga columbiana*), a relatively asocial seed-caching corvid. The nutcracker stores and recovers tens of thousands of pine nuts every winter using its exceptional spatial memory. Nutcrackers may have a relatively sophisticated ability to discriminate numbers of things, given their strong dependence upon caching and recovering nuts for their survival. I presented two sets of nuts simultaneously, in 21 different conditions, to see if the nutcrackers could choose the larger of the two quantities. The nutcrackers displayed a strong ability to discriminate quantities of nuts and successfully chose the larger of two quantities in 20 out of the 21 conditions. Like many other animals tested previously, the nutcrackers showed a ratio effect, with performance decreasing as the ratio of the two quantities approached 1. Interestingly, nutcrackers did not show a significant effect of magnitude; at constant distances they did not have more difficulty with contrasts containing larger numerosities. I speculate that nutcrackers, like several large brained social mammals, might be using an analog magnitude representational system. These birds may have developed a keen number sense as an adaptive specialization to cope with their unique ecological pressures.

Introduction

The ability to discriminate numbers of things, far from being an exception, is widespread in the animal world. Laboratory and field experiments have shown that many diverse species demonstrate this basic understanding of numerosity (reviewed in Gallistel 1989, Dehaene 1997, Uller 2008). The ability to discriminate "less" versus "more" has been demonstrated in many animals, such as lions (*Panthera leo*, McComb et al. 1994), howler monkeys (*Alouatta caraya,* Kitchen 2004), horses (*Equus caballus*, Uller and Lewis 2009), dolphins (*Tursiops truncatus,* Mitchell et al. 1985, Kilian et al. 2003, Jaakkola et al. 2005), dogs (*Canis familiaris,* Ward and Smuts 2007), sea lions (Otaria *flavescens,* Abramson et al. 2011), and salamanders (*Plethodon cinereus*, Uller et al. 2003). A number of researchers have examined the underlying cognitive processes that would support relative number discriminations in non-human animals. Many studies have indicated that humans (i.e. Feigenson et al 2002) and animals (i.e. Hauser et al. 2003) represent numerosities in accordance with Weber's Law, which states that the larger the difference between two quantities to be discriminated, the easier it is to discriminate them. This is called the "distance" (or disparity) effect. Furthermore, the ratio of the two numbers is of paramount importance, with ratios of 1:2 being easier to discriminate than 3:4. For example, 6-month-old human infants can discriminate 8 from 16 objects (ratio of 1:2), but not 8 from 12 objects (ratio of 2:3; Xu and Spelke 2000). A variety of animals also show ratio and distance dependent behavior (e.g. Agrillo et al. 2009, 2010; Brannon and Terrace 2000; Buckingham et al. 2007; Cantlon and Brannon 2006; Dehaene 1997; Gallistel 1989; Gómez-Laplaza and Gerlai 2011; Meck and Church 1983; Vallortigara et al. 2010). In addition to distance and ratio effects, animals also often exhibit a magnitude

effect. The magnitude effect describes the phenomenon that at a constant numerical distance, accuracy is better with small rather than large numerosities. In other words, larger numbers of things tend to be more difficult to discriminate. Beran (2007) tested rhesus macaques (*Macaca mulatta*) using a computer and joystick. Two different quantities of stimuli (red squares) dropped down into two simulated containers, and the monkeys were required to respond to the larger. The monkeys were tested on all combinations of the numbers 1 to 10 over many trials. At constant distances, they were more accurate with combinations that were of small magnitude (i.e.1v2) than of a large magnitude (i.e.7v8).

While scientists are currently trying to understand how animals represent numbers, they are also interested in the evolutionary processes which might explain how number competence became so prevalent in the animal kingdom. The ability to discriminate among different quantities of objects could have arisen either through divergent or convergent evolutionary processes. If divergent evolution were the driving force, then an ancient common ancestor (possibly before the split of fish and amphibians or earlier) may have developed number sense, and then this homologous trait was passed to all future generations (Emery 2009). On the other hand, in a convergent evolution model, vastly different species could have developed number sense independently (homoplastic trait) to cope with common problems in their environment, like finding food and avoiding predators (Keeton & Gould 1986, Seed at al 2009, Scarf et al. 2011). Several convergent hypotheses may explain how factors in the environment might drive number cognition in various species, since the need to discriminate between large and small quantities may be ubiquitous. The "adaptive specialization" hypothesis posits that

animals may have evolved specific cognitive traits, such as numerical abilities, to adapt to problems in their environment (Kamil 1987; deKort and Clayton 2006). For example, unrelated animals that cache food (i.e. rodents, birds etc.) may have had increased pressure to keep track of quantities of food. Thus, for these animals, number sense might be an adaptive specialization (Mikolasch et al. 2011). In another model, animals living in large social groups may have acquired advanced cognitive abilities due to the pressures of living in a complex social network. According to "social intelligence" hypotheses (i.e. social function of intellect, Humphrey 1976; social brain hypothesis, Dunbar 1998), social species should be more likely to develop complex cognitive traits (like keeping track of the number of allies, etc.) than more solitary species.

In the current study, I examined the ability of Clark's nutcrackers to discriminate between two quantities of pine nuts (*Nucifraga columbiana*). Nutcrackers cache 33, 000 or more nuts each autumn (Lanner 1996), and are able to locate and recover most of them (Balda & Kamil 1992). Remembering where their nuts are hidden is crucial for the nutcracker's ability to survive during the course of the winter in the extreme cold of the high alpine regions where they dwell. Although empirical studies with birds in the family Corvidae (crows and their relatives) suggest that they possess many aspects of intelligence previously ascribed only to primates (i.e. manufacture and use of tools, inferential reasoning, etc.), few studies have examined numerical cognition in this family. In the only other study of numerical ability in nutcrackers, the birds were required to locate an object on the basis of its ordinal position in a series of identical objects. The nutcrackers were trained to locate the 4^{th} and 6^{th} object in a series of 16. They chose the correct object significantly above chance in both conditions, based on its ordinal position.

Interestingly, during this task the nutcrackers always began at the left and not the right end; in other words, they seem to count from left to right, as do humans (Rugani et al. 2010). Because of their need to keep track of a large number of caches and items within a cache, a sense of numerosity may be particularly well developed for nutcrackers compared to other corvid birds. Indeed, spatial cognition (Kamil & Balda 1985, Gibson & Kamil 2001a and b, Gibson & Kamil 2005, Gibson & Shettleworth 2003) is believed to be controlled by the same brain areas or with the same neural circuits as numerical cognition (Dehaene 1997). Therefore, animals like the nutcracker, for which spatial memory is an adaptive specialization, might also be expected to be proficient in their knowledge of number.

Methods

Animals

Five adult nutcrackers (undetermined sex) were trapped in western North America and housed individually at the University of New Hampshire, in an environmentally controlled room (22° C, 14:10h light: dark cycle). The birds had previously been used in several different experiments, (Gibson and Kamil 2001a &b; Gibson and Kamil 2005; Tornick et al. 2011; Tornick and Gibson, inferential reasoning, under review); none of which examined number cognition. The birds were maintained at 90% of their free-feeding weight, by regulating intake of turkey starter, pigeon pellets, striped sunflower nuts, and mealworms following experimental sessions, and had unlimited access to grit and water. For the duration of the experiment, their daily ration of pine nuts (a favorite food) was given during training or testing sessions only.

Apparatus

For familiarization, training, and testing, I transported the birds from their home room to an adjacent testing room in the same building. I trained and tested the nutcrackers individually in a cage measuring 45 cm wide x 45 cm long x 60 cm high (Figure 6). A single wooden perch sat 10 cm above the floor of the cage. The whole cage sat on a small wooden table measuring 45 cm wide x 70 cm long x 80 cm high. I positioned two small wooden choice trays (12 cm wide x 8 cm long x 2 cm high) on the table in front of the cage. Each choice tray had a well (5 cm wide x 5 cm long x 0.6 cm deep) that was lined with black rubber matting and had a hinged transparent Plexiglas® cover. The purpose of the rubber matting was twofold, it provided a visual contrast to make the light colored pine nuts more prominent, and it kept the nuts from slipping in the wells when the trays were moved. The Plexiglas® lid allowed a subject to see into the food well, but had to be lifted by the bird in order to access the contents of the well. I attached a handle to the front edge of the choice trays, so that I could manually slide the trays into (made accessible to subject) or out of the cage (made inaccessible). I added a movable wooden barrier (45 cm long x 12 cm high x 0.6 cm thick) outside the cage at the bottom so that the birds could not escape through the front (where the choice trays would be slid in and out). I affixed an opaque black curtain at the top of the front of the cage. To prevent accidently cueing the birds, I lowered the curtain when the bird made a choice (see procedures below) so that the experimenter was out of sight. I mounted an overhead Microsoft VX-6000 LifeCam video camera to the top of the cage, which I used to view and record the birds' choices via a Dell Inspiron 6400 laptop computer.

Familiarization

During familiarization, I gave each bird one daily session consisting of 16 trials in

the experimental apparatus. I placed a single ½ pine nut under the Plexiglas lid in the well of one of the sliding trays, and slid the tray into the cage. The subject could approach the tray and lift the Plexiglas® lid with its beak to obtain the nut inside. After one week, all five birds were quickly opening the lid to extract the pine nut.

Training

During each trial, I placed the bird in the experimental cage and lowered the opaque curtain. The experimenter sat in a chair in front of the apparatus, and placed one, two or three pine nuts under the Plexiglas® lid in the well of one of the two sliding trays (the other tray remained empty). Even though only one of the two food wells in the trays was baited, the experimenter opened and closed the lid of the unbaited, as well as the baited food well (randomized which side was manipulated first). I also randomized which side was baited and the number of pine nuts (~5 trials per daily session for a total of 8-10 pine nuts) that were placed into the food well of one of the trays. Once one of the trays was baited, the experimenter simultaneously slid both trays into the cage. The subject was allowed to make a single choice. I recorded a choice when a bird first touched a lid on one of the food wells with its beak. As soon as a choice was made, the experimenter slid the unchosen tray out of the cage. If the subject chose the baited food well (considered a correct choice), it was allowed to consume the pine nuts. If the bird chose the empty food well (an incorrect choice) it received no reinforcement, and I repeated the trial. I recorded the birds' choice (baited or empty, left or right side) for each trial. I required a minimum of 7 out of 8 correct choices for 5 consecutive days before proceeding to testing.

Testing

Testing took place between 8 and 10 A.M. daily, prior to maintenance feeding. The testing procedures were the same as training except that, instead of one of the wells in one of the trays being empty, I baited the two food wells with different quantities of pine nuts. I distributed the nuts pseudo-randomly on the black matting in the food wells. Both sets of nuts were visible during the entire trial, a procedure that has previously been used for birds (e.g., African grey parrots, Al Aïn et al. 2009). I added an additional clear Plexiglas® panel (40 cm long x 10 cm wide x 0.3 cm thick) on top of both choice trays. The purpose of this panel was to allow the birds to see the contents of the baited food wells, but prevent them from making a hasty choice. At the start of a trial, the experimenter placed the Plexiglas® panel over the two sliding trays. The experimenter then simultaneously slid the panel and the two choice trays into the cage. After a one minute delay the experimenter slid the Plexiglas® panel out of the cage and the bird was allowed to select one of the wells by lifting the Plexiglas® lid with its beak. Just as in the training phase, as soon as the bird made a choice, the experimenter slid the unselected food tray out of the cage, so that only one choice could be made per trial. After the bird ate the contents of the chosen food well, the experimenter slid that tray away and the trial ended. For each trial, I recorded the birds' choice (larger or smaller, left or right side). If a bird chose either the larger (designated a correct choice), or the smaller (designated an incorrect choice) of the two quantities, it was allowed to consume all of the pine nuts from that pile. I did not administer correction trials.

I tested the birds' ability to discriminate the following ratios: 1v2, 1v3, 1v4, 1v5, 2v3, 2v4, 2v5, 3v4, 3v5, 3v8, 4v5, 4v6, 4v8, and 5v6. I presented each bird with between three and five of these ratios (random order) per daily session, for a total of 8-10 pine

nuts each day. I counterbalanced the side holding the larger quantity, and the larger quantity was not presented on the same side for more than two consecutive trials. Each bird encountered each ratio eight times, over a period of 25 days. After I conducted these tests, I extended testing to include seven additional ratios: 6v7, 6v8, 6v9, 6v12, 8v9, 8v10, and 8v16. To avoid overfeeding I presented ½ instead of whole pine nuts, for these new ratios. I cut the pine nuts so that they were uniform in size (best visual estimate). Each bird encountered two or three of these conditions per day (random order) and encountered each of these new conditions a total of eight times (over an additional 25 days).

Control Tests

To see what stimulus features were important for the birds' choices, I ran three types of control tests: *Number*, *Volume*, and *Area.* In the *Number* condition, I presented the birds with two quantities of food that had an equivalent volume, but one tray had a larger number of nuts; 1 whole nut *vs.* 2 halves, 2 whole *vs.* 4 halves, and 3 whole *vs.* 6 halves. I attempted to ensure that the volumes of nuts in the two trays were equivalent (best visual estimate), and that the whole array took up the same amount of area.

During the *Volume* control tests I wanted to know whether the birds would be able to choose by volume when the number of nuts and the area occupied by the food on the tray was held constant. I examined three conditions: 1 whole *vs.* 1 half nut, 2 whole *vs.* 2 half nuts, and 3 whole *vs.* 3 half nuts. Here I tried to keep the area of the array constant (note that this is not possible in the case of 1 whole *vs.* 1 half, so volume may be confounded with area in that particular condition only).

Using the *Area* control tests I wanted to know whether the area occupied by the

nuts on a tray, when the number and volume of the nuts were held constant, would control behavior. I tested the birds with three conditions: 2 whole nuts in a small array (~ 5mm spacing between nuts) vs. 2 whole nuts in a large array (~3cm spacing between nuts), 3 whole nuts in small array vs. 3 whole nuts in large array, and 4 whole nuts in a small array vs. 4 whole nuts in a large array.

I conducted the trials in the *Number, Volume*, and *Area* control conditions using the same procedures for testing described above. I randomized the order of presentation of the control type and the conditions, and randomized the tray in which the larger number, volume, or area of nuts was presented. I gave the birds 4 or 5 trials per daily session (for a total of 8-10 pine nuts), and tested them 8 times with each condition over a 17 day period. For each trial, I recorded the birds' choice (larger or smaller, left or right side). The subject was allowed to consume all of the pine nuts from whichever pile it chose. I did not use correction trials during these control tests.

Analysis

I determined the percentage of occasions that a nutcracker selected the tray with the larger number of nuts for each of the conditions used during testing. I conducted binomial tests to examine whether the number of occasions that the nutcrackers selected the food well with the larger number of nuts was greater than expected by chance for each of the conditions used during testing. Next, I plotted the percentage of choices for the larger of two quantities of nuts as a function of the ratio index; a measure of the proportion of nuts in the two food wells during a test (ratio index = smaller number of nuts/ larger number of nuts). I then performed a linear regression using the percent choice scores as one factor and the ratio index as a second factor to assess if the choices made by

the nutcrackers changed as a function of task difficulty (increasing ratio index). I performed a second regression to determine if the distance (disparity) between the two quantities of nuts in each tray influenced the choices made by the birds. I created a distance index by determining the absolute difference in the number of nuts in the two trays. I then used the distance index and the percentage of tests that the birds selected the larger quantity of nuts as factors in the regression. I performed a third regression to determine if, at constant distances, the increasing magnitude of the numbers in the pair influenced the choices made by the birds. To do this I created a magnitude index by summing the two quantities of nuts in each tray for each test. Then I organized the data into three categories based on the distance of the two quantities: constant distance of 1 (i.e. 1v2, 2v3 etc., N=7), constant distance of 2 (i.e. 1v3, 2v4 etc., N=6), and constant distance of 3 or more (N=8). For each of these three categories I used the magnitude index and the percentage of tests that the birds selected the larger quantity of nuts as factors in the regression.

Finally, I used binomial tests (2-tailed) to examine if the percentage of choices for the larger of the two quantities in each food well was significantly more or less than expected by chance for each of the *Number*, *Volume*, and *Area* control conditions.

Results

The nutcrackers selected the larger of the two quantities of nuts significantly more often than would be expected by chance during all of the ratios (Table 1, all $ps < 0.05$) except the 8 vs. 9 condition (during which they performed at a chance). The data from individual birds also is consistent with this trend. The regression analysis I performed using the ratio index for each condition and the percentage of choices for the larger

quantity of nuts revealed a significant negative linear relationship between these two factors ($R^2 = 0.429$, $\beta = -29.35$, $p = 0.001$; Figure 7, left panel). Thus, as the ratio between the numbers of nuts in the two food wells increased (became more difficult) the ability of the nutcrackers to discriminate between them became more difficult. The impact of distance, that is the difference in the number of nuts in the two piles, was less pronounced. The birds did show a trend of selecting the larger of the two quantities of nuts as the distance between the two quantities increased (Figure 7, right panel). However, the impact of distance on choice was just outside my criterion for statistical significance ($R^2 = 0.157$, $\beta = 1.923$, $p = 0.076$). As can be seen in Figure 8, at constant distances, the birds were just as good at discriminating conditions with small and large magnitudes. Correspondingly, there was no significant effect of magnitude at a constant distance of 1 ($N = 7$, $R^2 = 0.275$, $\beta = -1.034$, $p = 0.227$; Figure 8), a constant distance of 2 ($N = 6$, $R^2 = 0.050$, $\beta = -0.311$, $p = 0.669$; Figure 8), or a constant distance of 3 or more ($N = 8$ $R^2 = 0.150$, $\beta = -0.432$, $p = 0.342$; Figure 8).

During the *Number* control condition (when the volume of the nuts and the area they occupied was held constant), the birds chose the food well with the smaller number of nuts significantly more often than would be expected by chance (Mean = 0.35, SE = 0.055, $p = 0.001$; Figure 9). In the *Volume* control condition, the birds had a strong preference for choosing the food well with the greater volume (Figure 9) when number of nuts was held constant but the volume of one set of nuts was increased (Mean =0.925 SE = 0.036, $p < 0.001$). In the *Area* condition, the nutcrackers chose the food well with the smaller area of nuts (Figure 9) more often than expected by chance (Mean = 0.425, SE = 0.060, $p = 0.030$) when the volume and number of nuts were both held constant. Results

for individual birds are shown in Table 2.

Discussion

In the current study I tested the ability of Clark's nutcrackers to make a relative number discrimination by choosing the larger of two quantities of pine nuts. I tested a large number of conditions, and used quantities of higher magnitudes than are typical in these types of tests for animals. The nutcrackers' performance was significantly above chance for 20 out of the 21 conditions that I examined. Thus, even for very fine discriminations, the nutcrackers were adept at choosing the larger pile. Compared to many other animals tested with a similar paradigm, the nutcrackers performance appears to be quite sophisticated. Previous studies of various species, mostly large brained social mammals including primates, have consistently demonstrated that the ability to discriminate between two quantities is limited to a maximum set size of four (reviewed in Gallistel 1989, Dehaene 1997). Exceptions to the set size limit of four have been shown in dolphins (Jaakkola et al. 2005), Asian elephants (*Elaphus maximus,* Irie-Sugimoto et al. 2009) and one individual African grey parrot (Pepperberg, 2006). The nutcrackers in this study, on the other hand, were proficient at contrasts including up to 8, 10 and even 16 items. Thus, within the animals tested so far, Clark's nutcrackers appear to be at the high end of the spectrum with regard to number discrimination abilities.

I am not aware of other tests of number discrimination using this paradigm in birds. However, experiments using different procedures suggest that many birds are able to discriminate quantities of objects. For example, female brown-headed cow birds, an obligate brood parasite, prefer to lay eggs in host nests containing three eggs as opposed to nests with only one egg (White et al. 2007). Black-capped chickadees, *Poecile*

atricapillus, change the number of "chicks" and "dees" in their vocalizations depending on the perceived level of threat of a predator (Templeton et al. 2005). Ravens and jackdaws discriminate temporal vocalizations on the basis of number of elements (Koehler 1951). The cawing of crows also appears to be based on a simple number scale with an upper limit of about six (Thompson 1969). Thus, number sense might form the basis of communication in these species of birds. In a recent study, pigeons were trained to rank order pairs of stimuli consisting of one, two, or three elements (shapes or pictures on a computer screen). When tested with novel pairs of stimuli (quantities ranging from 1 to 9), pigeons were significantly above chance in the novel pairings (Scarf et al 2011). The results of my study, in conjunction with those of Scarf's group, seem to support the notion that unlike most mammals, which can discriminate a maximum of only four objects (except elephants and dolphins, which can discriminate up to 6 items), discrimination of a larger number of objects may be possible among birds.

The nutcrackers in this study showed a ratio effect, but no significant effects of distance or magnitude. The birds' ability to discriminate between the two quantities, while remaining above chance, declined as the ratio between the quantities became finer (as predicted by Weber's law). Thus they demonstrated a ratio effect that is consistent with results from other animals (e.g. Agrillo et al. 2009 and 2010; Brannon and Terrace 2000; Buckingham et al. 2007; Cantlon and Brannon 2006; Gómez-Laplaza and Gerlai 2011; Meck and Church 1983; Vallortigara et al. 2001). Other birds also seem to demonstrate a ratio effect. For example, Scarf and colleagues (2011) found that pigeons' (rank ordering of novel pairs of shapes on a computer screen) performance also declined with tighter ratios. For the nutcrackers in the current study, the distance effect was less

pronounced. The nutcrackers showed a slight (non-significant) tendency for increased accuracy as the distance (disparity) between the two numerosities increased. In contrast, in at least two studies, pigeons showed a significant distance effect. Roberts (2010) presented pigeons with red and green lights that appeared briefly in sequence, with the more frequent stimulus defined as 'A' and the less frequent stimulus defined as 'B'. The pigeons were required to choose a comparison stimulus that was the same color as the more frequent of the two stimuli. Three experiments clearly indicate that the pigeons' behavior is governed by a distance effect. In a similar study, Scarf and colleagues (2011) found that when rank-ordering novel pairs of shapes on a computer screen, pigeons were more accurate as the distance between the numerosities of a pair increased. Although it is difficult to make comparisons across species from studies using these different paradigms, it is possible that nutcrackers are more accurate than pigeons when the distances between the two numbers to be discriminated are small.

The nutcrackers in the current study did not demonstrate a significant effect of magnitude for the conditions I tested. At constant distances, they were able to discriminate large quantities as successfully as smaller quantities. The only other animal that I am aware of that also does not show a magnitude effect is the Asian elephant (*Elephas maximus*). When tested with similar procedures as in the current study, elephants successfully discriminated objects up to a quantity of six; and only one of the nine elephants showed a magnitude effect (Irie-Sugimoto et al.2009). Thus, like the nutcrackers in the current study, most elephants did not have increasing difficulty with larger numbers (at a constant distance of 1, 3v4 was no more difficult than 1v2), despite the fact that more total food was available in the larger contrasts. In contrast, in one of the

few studies to examine this effect in birds, Robert's (2010) pigeons showed a significant magnitude effect when choosing the more frequent of two stimuli.

To determine which features the nutcrackers may be relying on to make choices, I also conducted three additional types of tests (*Number*, *Volume*, and *Area* controls). In the *Number* controls, I simultaneously presented the birds with two different quantities of pine nuts, but held the volume of food and the area of the two choices at a constant. Contrary to my expectations, the birds mostly chose the smaller number of items (i.e. they chose 1 whole nut over 2 half nuts). I expected the nutcrackers performance to be similar to that of young human children. Before reaching Piaget's concrete operational stage (around age 6 or 7), children prefer two half graham crackers over one whole graham cracker (i.e. Cordes and Brannon 2008). When asked why they make this choice, they explain that "two is more than one". The nutcracker's behavior seems to be more consistent with that of human adults, who also seem to prefer unbroken food when given a choice (i.e. Geier et al. 2006). The nutcrackers' behavior may also be consistent with optimal foraging theory (MacArthur and Pianka 1966), which states that organisms forage in such a way as to maximize their net energy intake per unit time. In order to forage optimally, nutcrackers may be hardwired to choose whole nuts, because broken pieces may be of poorer nutritional value, more difficult to carry, or they may decay more quickly.

In the *Volume* controls, I simultaneously presented the birds with two different volumes of pine nuts, but I held the number and area (of the array) of the two choices at a constant. As I predicted, the birds overwhelmingly chose the quantity with the larger volume of food (i.e. they chose 2 whole nuts over 2 half nuts). This behavior is also

consistent with optimal foraging theory (MacArthur and Pianka 1966), because animals should be able to assess food patches and determine which has a larger volume of food. It should be adaptive for animals to be able to discriminate the amount (volume) of food material, and ignore number of items. This preference for the larger amount is so prevalent that it is often referred to as the "natural choice procedure" (Silberberg et al. 1998).

In the *Area* condition, I simultaneously presented pines nuts in a large array and a small array, but held the number and volume of the nuts constant. The nutcrackers chose at chance in two of the three conditions; and chose the smaller array in one of the conditions (they chose 2 whole nuts that were close together over 2 whole nuts that were farther apart). This is contrary to my prediction that the nutcrackers might deem the larger array more appealing, as it may seem like more food. Unlike the nutcrackers in this study, young (pre-operational) human children commonly mistake a larger array of objects as "more". For example, children shown two rows containing an equal number of pennies believe that the longer row has a larger quantity. They continue to hold this misconception even if the rows start out at the same length and then one of the rows is then spread further apart, and even after they have counted the pennies. Unlike young human children, the nutcrackers behavior (at chance or choosing the smaller array) seems to suggest that they are aware of the equivalence of the nut material in both sets. One reason that the nutcrackers may have chosen the smaller array in one of the three conditions is that to forage optimally, animals should select a patch in which food items are close together; thus searching/handling time is decreased and energy intake is increased.

It is not yet clear which evolutionary factors may have been responsible for the development of such a keen number sense in nutcrackers. The Clark's nutcracker is a relatively asocial corvid, yet it demonstrates advanced number comprehension. Their ability to discriminate among numbers is as good (or better) than those of much more social birds (i.e. pigeons, Scarf et al. 2010) and mammals. Thus, living in a large social group does not appear to predict proficiency at discriminating numbers; and social intelligence hypotheses are not supported. One clue about how advanced number comprehension may develop in a species may stem from the fact that both elephants (Rensch 1957, Foley et al. 2008) and nutcrackers have remarkable long-term memory, and both seem to excel at number discrimination. For example nutcrackers cache up to 33,000 seeds each season, and need to remember their locations to retrieve them several months later. This increased pressure to keep track of such a large number of nuts over long distances may have driven the development of enhanced number cognition, as an adaptive specialization, in the nutcracker. Similar results from these two very distantly related organisms (nutcrackers and elephants) suggests that these unrelated animals with similar evolutionary pressures developed enhanced number cognition as a homoplastic trait (convergent evolution model). This in turn could suggest that numerical and spatial cognition may be controlled by the same brain areas or neural circuits. Imaging studies suggest that the intraparietal sulcus may control both number cognition and spatial memory (Dehaene 1997). The hippocampus also is important for spatial memory; and neuroimaging work suggests that it may also be involved in controlling number sense (van Opstal et al. 2008, Hubbard et al 2008). Research suggests that compared with other corvids, the nutcracker may have a relatively larger hippocampal volume to body size

ratio (Krebs et al. 1989, Sherry et al.1989, Basil et al. 1996).

Scientists have also been interested in how animals represent numbers in memory. Two main representational systems have been posited, the object-tracking system and the analog-magnitude system. In object-tracking, animals represent small numbers as discrete numerosities in an "object-file" or "mental slot" (Uller 2008). Because of the small capacity of these "files", animals using this system are limited to a set size of about four (i.e. Feigenson et al., 2002, Hauser et al. 2003, Uller et al. 2001, McComb et al. 1994; Kitchen 2004; Uller and Lewis 2009; Uller et al. 2003, Mitchell et al. 1985, Kilian et al. 2003, Ward and Smuts 2007). The results from the nutcrackers do not support an object file model, as the nutcrackers were quite successful with quantities larger than four. The other possibility is that animals represent numbers using an analog magnitude system in which objects are represented in a less precise way (Dehaene 1997, Shettleworth 2010). In this model it is not necessary for animals to recognize absolute numbers or to label each separate object (e.g., Meck and Church 1983). Thus, if using an analog-magnitude system, an animal will presumably be able to discriminate quantities larger than four. The behavior of the nutcrackers in the current study, as well as that of sea lions (Abramson et al. 2011), dolphins (Jaakkola et al 2005), and elephants (Irie-Sugimoto et al 2009) in other studies may be consistent with an analog magnitude system of representation.

Conclusions

The ability of many diverse animal species to comprehend numbers may represent the evolutionary underpinnings of the more sophisticated numerical skills found in humans, yet the origins of numerical cognition remain unclear (Uller 2008; Shettleworth 2010). Here I present evidence for the tendency of a bird species, the Clark's nutcracker,

to select the larger of two simultaneously presented sets of food items, for set sizes up to 16, in manner that may exceed the abilities of many large brained social mammals (including apes). The nutcracker has a unique set of ecological pressures that may have driven the development of a proficient number sense. Because the nutcracker is relatively asocial, it does not appear that living in a large group influences the development of a keen number sense. Rather, the nutcrackers' skill at discriminating numbers may be tied to its remarkable spatial memory, both from an evolutionary standpoint, and a neurological one. Additional tests of numerical ability in nutcrackers and related corvids (as well as other animal that store and do not store food) will be important to help us understand which pressures drive the evolution of numerical cognition, and which mechanisms and representational systems are utilized.

CHAPTER IV

AN INVESTIGATION OF CACHE-PROTECTION BEHAVIOR IN THE ASOCIAL CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA*)

Abstract

I examined cache-protection behavior in the Clark's nutcrackers, a relatively asocial corvid bird. Past work with scrub jays indicates that this social corvid flexibly uses cache-protection strategies when they are observed making caches. I conducted several experiments to test whether nutcrackers, like scrub jays, alter caching and recovery behavior when observed, by caching food in locations that are far away from an observer, that are dimly lit, and that are behind a visual barrier. I found that, like scrub jays, nutcrackers engage in several different cache-protection behaviors (i.e. they preferentially cache in far locations and recover from in-view locations when they had been observed caching). The nutcrackers caching behavior was not affected by pilfering experience. Furthermore, the nutcrackers engaged in other behaviors that suggest social intelligence, such as increasing both caching frequency and caching rate in a hidden location when observed making caches. Increased activity in an in-view tray, with little caching there also suggests that the nutcrackers may have been exhibiting cache-guarding or false-caching behaviors. However, unlike scrub jays, the nutcrackers in this study did not increase caching in general when they were observed, nor did they suppress caching. Overall, nutcrackers cached more nuts and recovered a larger proportion of nuts that they

had cached, in comparison with scrub jays. Although there are some slight differences in the cache-protection behavior of the relatively asocial Clark's nutcracker and the more social scrub jay, both species seem to employ many similar (and some unique) cache-protection strategies. Thus, I suggest that group size may be a less important predictor of social intelligence than foraging pressures related to caching.

Introduction

Social intelligence hypotheses (i.e. social function of intellect, Humphrey 1976; social brain hypothesis, Dunbar 1998) posit that living in complex social groups may enhance the cognitive repertoire of an organism. Being aware of the behavior of others and modifying one's own behavior in the presence of others may provide a number of advantages (Kraus & Ruxton 2002), such as increased mating opportunities (King and Cowlishaw 2007), predator avoidance (Jolly 1996), and foraging advantages (King and Cowlishaw 2007). Social animals have been shown to alter their behavior in the presence of others (Seed et al. 2009). For primates, there is evidence that group size is correlated with relative brain size, and living in large groups also predicts complex cognitive capabilities (Barett et al. 2002, Barton 1996; Dunbar 1998; Reader and Laland 2002; MacLean et al. 2008; Isler and van Schaik 2009). However, it is yet to be determined if social intelligence hypotheses can be extended to groups of animals other than primates.

A few studies have examined social intelligence hypotheses in birds. For example, Bond and colleagues (2003 and 2010) examined one cognitive feature, transitive inference, in several species of corvid birds living in groups with varying degrees of social complexity. They found that highly social pinyon jays (*Gymnorhinus cyanocephalus*) showed an increased ability to use transitive inference to track multiple

dyadic relationships, compared with moderately social western scrub-jays (*Aphelocoma californica*). In another comparative study, Templeton, Kamil, and Balda (1999) tested relatively asocial Clark's nutcrackers (*Nucifraga columbiana*) and pinyon jays using both a motor task and a discrimination task to examine social learning. Nutcrackers learned faster individually than pinyon jays, while pinyon jays learned faster socially than nutcrackers. Lefebvre's group (1997) found that in various species of North American and British birds, feeding innovation and opportunism were correlated with increased forebrain size. These cumulative results provide some evidence supporting social intelligence hypotheses in birds. Yet much more work is needed.

To examine whether social organization plays an important role in predicting social intelligence in birds, it is important to conduct comparative research examining social intelligence across closely related species of birds that differ with respect to social group size. One potentially fruitful line of research is to study birds that cache food to see if they alter their behavior when they are observed caching by another individual (a gauge of social intelligence). Caching is the act of storing food (long-term or short-term) in times of plenty, to be recovered and utilized in times of scarcity. Many corvid species (crows and their relatives) regularly cache and pilfer food; and there is a good deal of evidence suggesting that they use cache-protection behaviors flexibly, depending on the specific social context of a caching event. For example, when observed caching, several corvids increase or decrease caching activity (increase- Eurasian jays, *Garrulus glandarius*, Bossema 1979; decrease- Northwestern crows, *Corvus caurinus*, James & Verbeek 1984; ravens, *Corvus corax*, Heinrich & Pepper 1998, Bugnyar & Kotrschal 2002; rooks, *Corvus frugilegus,* Simmons 1968; grey jays, *Perisoreus canadensis,*

Burnell & Tomback 1985). Ravens (Bugnyar and Heinrich 2005) and magpies *(Pica pica*, Clarkson et al. 1986) prefer to cache out-of-view or in difficult-to-see locations when they are observed. Other corvids alter the spacing of a cache when observed (magpies, Clarkson et al. 1986; grey jays, Waite & Reeve 1995), repeatedly move their caches, or move their caches during private recovery sessions (Eurasian jays Goodwin 1955, Cramp & Perrins 1994; ravens, Heinrich and Pepper 1998). Some corvids also increase cache-protection after they have pilfered the caches of others (scrub jays Emery et al. 2004, Clark's nutcrackers, Clary and Kelly 2011).

A series of studies have extensively examined cache-protection behavior in the scrub jay, a relatively social corvid which lives in large flocks and is a generalist forager. For example, Dally, Emery, and Clayton (2004, 2005a and b) tested scrub jays by providing differential caching opportunities in both the presence and absence of an observer, to determine if they preferentially cache in locations that make it more difficult for an observer to see (and potentially pilfer) their caches. The results indicate that scrub jays preferred to cache food in locations far away from an observer, out-of-view, and in "shady" locations. These behaviors were exhibited when the birds cached with another bird present, but not when they cached in private. During a recovery period, they relocated more seeds that were cached near an observer, in-view, and in "sunny" locations. Thus, scrub jays behave as if they are aware of another individual's knowledge; perhaps they use this knowledge flexibly to confuse potential pilferers. One explanation for modifying behavior in the presence of others is an awareness of another's intentions, and may be a precursor to a theory of mind (attribution of mental states to oneself and others) (Premack and Woodruff 1978, Hare et al. 2001, Emery & Clayton 2008).

In order to use a comparative approach towards understanding the evolution of social intelligence by examining cache-protection behavior, it is imperative to conduct studies that include asocial species. A good candidate for such comparative studies is the Clark's nutcracker, which is considered the least social of the corvids. Compared to most other corvids which form large flocks and breed or nest cooperatively, the nutcracker forms only small flocks as juveniles (Mewaldt 1948, Tomback 1978). Breeding pairs are highly territorial (Mewaldt 1956). Foraging individuals prefer to cache alone rather than in groups, and they distance themselves from conspecifics by approximately one meter (Tomback 1978, 1998). Although less social than other corvids, nutcrackers would potentially still benefit from paying attention to other individuals and utilizing cache-protection strategies. But it is not known whether they are aware of others, or if they alter their cache-protection behavior flexibly as do more social corvids, like the scrub jay. Nutcrackers are known to occasionally pilfer each other's caches. However, Vander Wall (1982) and Bednekoff and Balda (1997) found that when nutcrackers observe another bird caching, they often have difficulty finding the food. This suggests that observational spatial memory may not have evolved in this asocial species. Clary and Kelly (2011) recently conducted a comparative study (a replication of a study with scrub jays, Emery et al. 2004) to examine how the experience of having one's cache pilfered affects subsequent caching behavior. They trained nutcrackers that any food cached in a tray that was near an observer would be "pilfered" (unavailable during recovery), but food cached in a tray that was far away from the observer was left intact (available during recovery). Nutcrackers that had previous experience with pilfering decreased the amount of caching, and recovered more nuts when they had been observed by a conspecific. This suggests

that nutcrackers, like more social scrub jays, may be sensitive to the presence of others and alter their caching behavior accordingly. Therefore, living in a large social group may not be a prerequisite for using cache-protection strategies flexibly.

The purpose of this study was to conduct a set of detailed experiments to determine whether asocial Clark's nutcrackers alter their behavior when another bird is present in a manner similar to more highly social scrub jays (Dally et al. 2004, 2005 a and b). Through of series of experiments, this study examines the influence of social group size on social intelligence (with regard to cache-protection) in caching corvids. I examined whether nutcrackers preferentially cache far away, in dimly lit locations, or behind a visual barrier, and whether they change their caching efficiency when observed. I predicted that even though nutcrackers are relatively asocial birds, they should prefer to cache nuts in locations that are far away from an observer, in "shady" locations, and out-of-view, but not when caching "in private". I examined whether the birds would preferentially recover a larger proportion of nuts that they had cached (while being observed) from locations that are brightly lit, near an observer, and in the observer's line of sight. I also examined the nutcrackers behavior in the presence and absence of food, to determine how social interactions without food differ from caching behavior. Lastly, I examined whether experience of pilfering others' caches and having their own caches pilfered would subsequently affect the nutcrackers' caching behavior. If the nutcrackers exhibit cache-protection behavior that is similar in nature to the more social scrub jay, the social intelligence hypothesis will not be supported. If nutcrackers exhibit similar cache-protection strategies as the scrub jay, it will suggest that the pressures of caching and pilfering, rather than sociality, may lead to social intelligence in both nutcrackers and

scrub jays.

General Procedures

Animals

Five captive wild-caught Clark's nutcrackers of undetermined sex and age were maintained (*ad libitum*) on a diet of turkey starter, rowdybush pellets, striped sunflower nuts, and mealworms (*Tenebrio molitor*). They also received 50 pine nuts during daily testing or training sessions, which they could eat or cache. During probe training, two of the birds exhibited caching behavior at free-feed weight; therefore they were maintained on a free-feed diet for the duration of the experiments. Three other birds did not cache at free-feed weight, so they were reduced to 90% of free feed weight (by adjusting the amount of grain mix), and then they began caching. Water and grit were provided *ad libitum*. The birds were housed in individual cages measuring 60 x 60 x 80 cm (w, d, h) in an environmentally controlled room (22° C, 14:10h light: dark cycle). All of the nutcrackers participated in previous experiments examining spatial cognition (during which they searched for, but did not cache pine nuts), gesture comprehension, inferential reasoning, and number discrimination (Gibson & Kamil 2001, Gibson & Kamil 2005, Tornick et al. 2011, Tornick and Gibson under review, Tornick and Gibson in preparation). However, all of the birds were experimentally naïve to caching and pilfering.

Apparatus

The apparatus used here is similar to that used to test scrub jays (Dally, Emery, and Clayton 2005a), but was made larger (by ~ 30%) for the larger nutcrackers. The experimental arena (115 cm wide x 115 cm long x 54 cm high) consisted of a wooden

platform covered in white laminate, with four wooden posts supporting plastic mesh on four sides and the top (Figure 10). Birds were added and removed through a mesh flap on one side of the arena. A separate metal cage (115 cm wide x 54 cm long x 54 cm high with a central perch) which could house a single conspecific observer was moved to either the left or the right side, adjacent to the arena. Two open rectangular plastic utensil trays (36 cm wide x 15cm long x 6 cm deep) filled with corn cob filings were provided for caching and recovering pine nuts. Each tray was made visually distinct by affixing a wooden block (~8 cm wide x 5 cm long x 2 cm deep) which served as a unique marker (a green alligator and a blue rhino block) along one of the long edges of the tray (Figure 11). To help the birds orient, the two trays were always placed such that the alligator was located on the left side of the rhino (with respect to the focal bird). During testing, a centrally located bowl contained 50 pine nuts, a large enough quantity to ensure that caching was not restricted due to availability. The caching trays were always positioned equidistant from the food bowl (see Figures 12, 14, and 16 for the spatial arrangement of the trays in each experiment). Training and testing took place in a separate room, adjacent to the room in which the birds were housed. An overhead camera Microsoft LifeCam was used to view and record the behavior of the birds from an adjacent room.

Familiarization

The birds were familiarized with the apparatus and caching trays (in a central location in the arena, and in private) and bowl of 50 pine nuts, for 15 minutes each day. During these daily sessions, the birds were free to explore the arena, and eat or cache the pine nuts. Birds were then removed from the caching arena, and fed a maintenance diet in their home cages. After a 24 hour retention period, the birds were allowed a 5 min

recovery period to either eat or re-cache nuts they had cached (no additional nuts were present). Once all five of the nutcrackers were reliably caching nuts (4 or more nuts cached for at least 5 sessions) testing began. This familiarization phase lasted a mean of 17.4 days (SE = 4.08).

Testing- caching and recovery

In each daily session, I placed a bird in the testing arena for 15 minutes with the two caching trays (see individual experiments for a description of the experimental setup) and the bowl of 50 pine nuts. The trials were in one of two conditions: *Observed:* the observer was a different individual Clark's nutcracker, or *Private:* no observer, the observer chamber was empty. Individuals were paired in pseudo-randomized order, so that each bird was observed once by each of the other four birds. I also modified the location of the observer's cage between sessions, to counterbalance the observer's location with respect to the left and right side of the caching arena. At the end of a 15 minute trial, I removed the birds and trays and recorded the number and exact location of each individual pine nut (both outside the trays as well as buried in the corn cob filings in the trays). I placed the birds back in their home cages for a 24 hour retention period, and fed them a maintenance diet. After the 24 hour retention period, the experimenter replaced the nuts and trays exactly as they were found, except that nuts found outside the trays were not replaced.

The next day, I allowed the cacher back in the chamber for a 5 minute private recovery period, in which they could re-cache or eat the previously cached nuts. After this recovery period, I recorded the number and location of any remaining nuts. I then removed the birds, brought them back to their home cages, and fed them a maintenance

diet (see above). If a bird cached fewer than four pine nuts in a caching session, the recovery procedure proceeded the next day; however I omitted both the caching and recovery data (this was a rare occurrence). For each experiment, each bird received four "observed" and four "private" trials as a cacher, in randomized order. The order of these trials and the identity of the observer were counterbalanced.

Experiment 1- Effect of Distance

One cache-protection strategy that an animal can use if it is sensitive to the presence of others is to hide food far away from an observer (potential pilferer). Caching far from an observer functionally decreases the amount of visual information available to the observer that can be used to locate a hidden cache. Recently, scrub jays were given the opportunity to cache in one of two caching trays, a tray that was near a conspecific observer or a tray that was farther away (Dally et al. 2005a). The birds were also tested in private. Dally's group (2005a) found that the scrub jays tended to cache in the far tray, indicating that they were sensitive to the presence of the observer. In this experiment, I used procedures similar to those used by Dally and colleagues (2005a) to test whether nutcrackers also prefer to cache far away from a conspecific, and to provide a direct comparison of the effect of distance on caching decisions made by the social scrub jay and the asocial nutcracker. I gave the nutcrackers caching and recovery opportunities in trays that were either near or far from an adjacent cage, in both observed and private conditions. If the nutcrackers are sensitive to the presence of a conspecific during caching, then they should hide more nuts in the far tray than in the near tray as was the case with the scrub jays, but show no preference in cache location when alone. Likewise, nutcrackers should also recover more nuts from the near tray when they had been

observed caching, than when caching had been in private.

Methods

I placed the two caching trays such that one was "near" and the other "far" from the observer cage (Figure 12). In the observed condition, the observer was free to move about its cage. After each 15 minute caching session, I recorded the number of nuts cached as well as their location (near or far trays). After each 5 minute recovery sessions (24 hours after caching), I also recorded the number and location of all nuts (in near or far trays).

Analysis. For the caching analysis, the dependent variable was the number of nuts cached in each tray. I used a general linear model (GLM), repeated measures analysis of variance (ANOVA). In the ANOVA I used session, social situation (observed or private), and tray (near or far) as variables. I used a Kolmogorov-Smirnov procedure to test for deviation from normal distribution; and Levene's tests to confirm homogeneity of variance. I used paired samples *t*-tests to compare the total number of nuts cached and recovered in private and when observed (to test for general suppression or increase of caching), and the total number of nuts cached in near or far trays (to test for a phobia for or attraction to the adjacent cage). Next, I used paired samples *t*-tests to compare the number of nuts cached in four comparisons: 1) far/observed *vs.* near observed, 2) far/private *vs.* near/private, 3) far/observed *vs.* far/private, and 4) near/observed *vs.* near/private. To control for inflation of P values, I used a Bonferroni correction and report obtained alpha (α_{obt}). To be consistent with previous studies (Dally et al 2004, 2005a), I report medians and interquartile ranges (IQR). Alpha was set at 0.05 to determine significant effects, and all tests were two tailed.

For the recovery analysis, I calculated the number of nuts recovered in each tray as the difference between the number of nuts the bird had cached 24 hours prior and the number of nuts left in that tray at the end of the 5 min recovery session, regardless of the number of nuts eaten or moved (as per Emery et al. 2004, Clary and Kelly 2011). Then I calculated the proportion of nuts recovered, by dividing the number of nuts recovered by the number of nuts that had been cached the day before. I then conducted the identical analyses for the recovery data as I did for the caching data, using the proportion of nuts recovered as the dependent variable.

Results and Discussion

Caching. The ANOVA revealed a near significant interaction between social situation x tray ($F_{1,4} = 6.36$, $P = 0.06$). No significant effects were detected for session ($F_{3,12} = 3.60$, $P = 0.08$), tray ($F_{1,4} = 5.377$, $P = 0.08$), social situation ($F_{1,4} = 4.77$, $P = 0.09$), or the interaction of session x social situation ($F_{3,12} = 0.94$, $P = 0.45$), session x tray ($F_{3,12} = 0.31$, $P = 0.82$), or session x social situation x tray ($F_{3,12} = 0.96$, $P = 0.44$).

The nutcrackers cached significantly more nuts in the far/observed condition (median = 9.5, IQR = 13.5) than the near/observed condition (median = 5, IQR = 8.5) (N = 20, $t_{19} = 3.42$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 13 left panel); however there was no significant difference in the number of nuts cached between the far/private condition (median = 8.5, IQR = 6.5) and the near/private condition (median = 12, IQR = 11.5) (N= 20, $t_{19} = -2.17$, $\alpha_{obt} = 0.01$, $P = 0.04$; Figure 13 left panel). The nutcrackers cached significantly fewer nuts in the near/observed condition (median = 5, IQR = 8.5), than in the near/private condition (median = 12, IQR = 11.5) (N = 20, $t_{19} = -3.61$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 13 left panel). They also cached more nuts in the far/observed condition

(median = 9.5, IQR = 13.5) than they cached in the far/private condition (median = 8.5, IQR = 6.5), but this difference failed to reach significance (N = 20, $t_{19} = 2.45$, $\alpha_{obt} = 0.01$, $P = 0.02$; Figure 13 left panel).

Overall there was no difference in total number of nuts cached by the nutcrackers when they were observed caching (total of far and near trays, N = 40) or when they cached in private; or total number of nuts cached in far (total of observed and private, N = 40) or near trays (*P*s > 0.05). The data were normally distributed, and did not violate the assumptions of homogeneity of variance.

Recovery. The nutcrackers, on the whole, recovered a large proportion of seeds that they had cached (median > 59% in all four of the conditions, Figure 13 right panel). However, there was no significant effect of session ($F_{3,12} = 1.27$, $P = 0.33$), tray ($F_{1,4} = 0.19$, $P = 0.69$), social situation ($F_{1,4} = 1.33$, $P = 0.31$), or the interaction of session x social situation ($F_{3,12} = 0.74$, $P = 0.55$), session x tray ($F_{3,12} = 2.01$, $P = 0.17$), social situation x tray ($F_{1,4} = 1.01$, $P = 0.37$), or session x social situation x tray ($F_{3.12} = 0.26$, P = 0.85).

There were no significant difference in the proportion of nuts recovered between far/observed *vs.* near/observed, far/private *vs.* near/private, far/observed *vs.* far/private, or near/observed *vs.* near/private (N = 20 for each group, all *Ps* > 0.05, Figure 13 right panel). Overall there was no difference in total number of nuts recovered by the nutcrackers when caching had been observed (total of far and near trays, N = 40) or when caching had been in private; or total number of nuts recovered from far (total of observed and private, N = 40) or near trays (*P*s > 0.05). Data were normally distributed and did not violate the assumptions of homogeneity of variance.

The nutcrackers altered their behavior by hiding more nuts in the tray that was far from an observer than they hid in the tray that was nearer to an observer. They also hid comparatively more nuts in the tray that was far from an observer than they hid in the tray that was far from an empty cage (and they hid fewer nuts in the tray near an observer than they hid in the tray near an empty cage). This seems to be similar to the cache-protection strategy (caching far from a conspeicifc when observed) used by the much more social scrub jay (Dally et al. 2005). Thus, cache-protection behavior may be adaptive both for animals that live in large social groups as well as for those that are less social. Interestingly, unlike scrub jays, which seem to increase caching when they are observed (Dally et al. 2005), the nutcrackers did not increase (or decrease) caching in the presence of an observer. The nutcrackers simply cached a large numer of nuts both when observed (19.5 of the 50 nuts availible in a 15 min session) and in private (18 nuts), but hid nuts preferentially in the far tray only when an observer was present. This is somewhat inconsistent with another study (Clary and Kelly 2011), in which naïve nutcrackers as well as those given pilfering experience actually decreased caching, both when caching was observed and in private (but not when caching in the presence of an inanimate object). In Clary and Kelly's (2011) study however, the private condition differed in that a conspecific was present, but behind a visual barrier. Thus, cachers could have detected auditory cues, and altered their behavior accordingly. Results from the current study suggest that nutcrackers that are naïve to pilfering do not increase or suppress caching in the presence of an observer, compared to when caching in complete privacy.

During recovery, the nutcrackers recovered a large proportion of the nuts that they

had cached in all of the conditions. However, the proportion of nuts recovered was not different when the nutcrackers had previously been observed making caches (median of 38.76%) than when they had cached in private (median of 50%). This seems to be different than the behavior that the scrub jays exhibited; the scrub jays increased recovery when they were observed and preferentially recovered nuts from the near tray when they had been observed caching (Dally et al. 2005a). It is not clear why scrub jays show more sensitivity (increased cache-protection) with regard to recovering their caches than the nutcrackers. Perhaps the nutcrackers are simply more efficient at recovery; recovering a larger proportion of nuts in general, without regard to the specific condition (observed or private) or caching tray (near or far). My results also differ from those obtained by Clary and Kelly (2011). In their study, naive and experienced nutcrackers recovered more nuts in the observed condition than they did when they had cached in private, or when they were observed caching by an inanimate object. It is not clear why I did not see a similar pattern of results in my study; rather the nutcrackers in the current study simply recovered a high proportion of nuts regardless of condition. One possibility is that in Clary and Kelly's (2011) study, the nutcrackers were given a 15 minute recovery period, compared to only 5 minutes in the current study. Thus, the nutcrackers in the current study may have eventually shown an increase in recovery in the near tray if they had been given more time (but then a direct comparison to scrub jays would not have been possible).

Experiment 2- Effect of Lighting

Another cache-protection strategy that an animal can use if it is sensitive to the presence of others is to hide food in difficult-to-see locations when an observer is present.

Dally, Emery, and Clayton (2004) gave scrub jays the opportunity to cache in either "sunny" or "shady" trays, in both private (an adjacent cage remained empty) and observed conditions. The scrub jays in that study preferentially cached in the shade when they were observed by a conspecific. To examine how social group size might affect cache-protection behavior, I tested caching decisions in the relatively asocial nutcracker using similar procedures as Dally's group (2004). As in Experiment 1, I again examined the number of nuts cached and recovered in bright and dimly lit trays (when caching was observed and in private) to see if the nutcrackers' caching behavior would be affected by the amount of illumination at the caching site, and whether they prefer caching in difficult-to-see locations when they are observed. If the nutcrackers are sensitive to others and alter their behavior when an observer is present, I should expect them to cache more nuts in the "shady" tray when observed as compared to the "sunny" tray (or compared to the shady tray when caching in private). They should also recover more nuts from the "sunny" tray than the "shady" tray when caching had been observed (and more than the sunny tray when caching had been in private).

Methods

The same birds and apparatus were used as in Experiment 1. An opaque barrier (30 cm wide x 4 cm long x 52 cm high) was added to separate the caching arena into two distinct sides (Figure 14); but both sides and both caching areas were equally visible and equidistant from the observer's cage. The caching arena also had two lamps each with a single 60w bulb, one on each side of the partition. The overhead room lights were turned off during testing; then on one side of the caching arena the lamp was turned off to create a "shady" caching area, while on the other side the lamp was turned on to create a

"sunny" caching area. The temperature of the caching substrate was 21° C on the shady side and 22.5° C on the sunny side. Over sessions, I counterbalanced which side of the chamber was "sunny" or "shady", as whether the observer cage was on the left or the right of the caching arena. I placed one cob-filled tray (with its distinctive markings) in the "sunny" side of the arena and the other in the "shady" side (see Figure 14). The observer was free to move about the cage. After each 15 minute caching session and each 5 min recovery session (24 hours after caching), I counted the number of cached nuts in each tray (sunny and shady trays).

Analysis. As in Experiment 1, for the caching data, I used a general linear model (GLM), repeated measures ANOVA, with session, social situation (observed or private), and tray (sunny or shady) as variables. I used paired samples *t*-tests to compare the total number of nuts cached and recovered in private and when observed, and the total number of nuts cached in sunny or shady trays (to test for a phobia or attraction to a particular illumination). Next, I used paired samples *t*-tests to compare the number of nuts cached in four pairwise comparisons: 1) shady/observed *vs.* sunny/observed, 2) shady/private *vs.* sunny/private, 3) shady/observed *vs.* shady/private, and 4) sunny/observed *vs.* sunny/private. For the recovery analysis, I used the same procedures as in Experiment 1. I examined the same pairwise comparisons as in the caching analysis (listed above), using the proportion of nuts recovered as the dependent variable.

Results and Discussion

Caching. No significant effect was detected for session ($F_{3,12} = 0.61$, $P = 0.62$), tray ($F_{1,4} = 2.36$, $P = 0.20$), social situation ($F_{1,4} = 0.61$, $P = 0.48$), session x social situation ($F_{3,12} = 0.43$, $P = 0.73$), session x tray ($F_{3,12} = 3.35$, $P = 0.08$), social situation x

tray ($F_{1,4} = 0.48$, $P = 0.53$), or session x social situation x tray ($F_{3,12} = 4.58$, $P = 0.06$).

Likewise, I did not find any significant difference between shady/observed *vs.* sunny/observed, shady/private *vs.* sunny/private, shady/observed *vs.* shady private, or sunny/observed *vs.* sunny/private (N = 20 for each group, all *P*s > 0.05, Figure 15 left panel). There was no difference in total number of nuts cached when the birds were observed caching (total of sunny and shady trays, N = 40) and the total number of nuts cached in private, or the total number of nuts cached in shady trays (total of observed and private, N = 40) and the total number of nuts cached in the sunny trays (*Ps* > 0.05).

Recovery. I did not detect any significant effects for session ($F_{3,12} = 1.87$, $P = 0.19$), tray ($F_{1,4} = 0.22$, $P = 0.67$), social situation ($F_{1,4} = 0.01$, $P = 0.97$), session x social situation ($F_{3,12} = 0.62$, $P = 0.62$), session x tray ($F_{3,12} = 0.75$, $P = 0.54$), social situation x tray ($F_{1,4} = 0.10$, $P = 0.77$), or session x social situation x tray ($F_{3,12} = 2.39$, $P = 0.12$).

The pairwise comparisons also indicated no significant differences between groups (N = 20 for all groups, all *P*s > 0.05, Figure 15 right panel). There was no significant difference between the total mean proportion of nuts recovered when caching had been observed (total or shady and sunny trays, N = 40) and the total mean proportion of nuts recovered when caching had been private (N = 40), or between the total mean proportion of nuts recovered from shady trays (total of observed and private, N = 40), and the total mean proportion of nuts recovered from sunny trays (N = 40) (*P*s > 0.05).

As in Experiment 1, the nutcrackers readily cached in both trays, and they cached a large number of nuts (i.e. overall mean = 23.5 out of 50, SE = 18.1) in the 15 minute caching period. However unlike Experiment 1, in which the nutcrackers altered their caching behavior when an observed was present, I did not see that pattern in this

experiment. Specifically, the nutcrackers did not demonstrate a preference to cache in the shady tray when an observer was present This contrasts with the behavior reported for scrub jays, which preferentially cached pine nuts in the "shade" when an observer was watching (Dally et al. 2004). Also, as in Experiment 1, in this experiment the nutcrackers again did not exhibit social suppression (or increase) of caching in the presence of an observer (median of 24.5 nuts out of 50 in a 15 min session when observed, and 22.5 nuts in private).

My data for nutcrackers could be interpreted in several ways. First, it is possible that the birds were not sensitive to the presence of the observer; however this is unlikely given that they demonstrated sensitivity to the presence of a conspecific in Experiment 1 (Effect of Distance). Second, it is possible that the nutcrackers were not sensitive to the difference between the sunny and shady trays, or that the difference in illumination was not great enough; again this seems unlikely as the nutcrackers have very acute vision (Gibson & Kamil 2005). A third possibility is that the propensity to cache in the shade to hide nuts from an observer, could have been counteracted if the nutcrackers generally prefer to cache in the sun. However, this is not supported because in the private condition, the birds did not show a preference to cache in the sun compared to the shade. The final possibility is that the nutcrackers did not consider caching in the shade to be an effective cache protection strategy. Since their vision is so keen, they may be able to see equally well in the shady and sunny trays. Extending this logic, they may have been able to project their experience onto the observer. Clayton and colleagues have suggested that scrub jays may be capable of experience projection, a form of theory of mind (Clayton et al. 2007; Emery & Clayton 2004, 2008). If a nutcracker possessed knowledge that, like

itself, the observing bird could clearly see into both the sunny and the shady tray, it may not show a preference for caching in either tray.

As in Experiment 1, the nutcrackers also recovered a large number of nuts that they cached, but they did not recover more nuts when they had been observed making caches. It is not clear how this behavior compares to scrub jays, because the scrub jays in Dally, Emery, and Clayton's (2004) study did not recover enough nuts for analysis. Therefore, it is inconclusive whether scrub jays preferentially recover more nuts from a brightly lit location when they are observed making a cache. However, I can tentatively conclude that neither nutcrackers nor scrub jays recover more nuts from a "sunny" tray (compared to "shady" tray) when they had been observed.

Experiment 3- Visual barrier and Pilfer experience

Another potential cache-protection strategy is to cache out-of-view of an observer. Dally, Emery, and Clayton (2005a) provided scrub jays with the opportunity to cache in either a location that was visually obstructed from an observer, or a location that was in the observer's line of vision. The scrub jays showed sensitivity to the presence of the observer by preferentially caching in the hidden location when they were observed, but not when they cached in private. Here I used similar procedures to determine if the less social nutcrackers would also show sensitivity to an observer. The nutcrackers were given the opportunity to cache and recover nuts either in a tray that was in plain view of the observer (in-view condition), or a tray that was located behind a visual barrier (hidden condition). If the nutcrackers are sensitive to others, then we should expect them to hide more nuts in the hidden tray when observed making caches compared to the in-view tray, and compared to when they cache in private. We should also expect the nutcrackers to

recover a greater proportion of the nuts that they had cached in the in-view tray compared to the hidden tray when their original cache-site had been observed, but not when caching had been in private.

Previous work with social corvids indicates that the experience of pilfering another's cache, or having one's own cache pilfered influences an animal's decisions regarding caching and recovering food stores. For example, individual hand-raised scrub jays that were given experience pilfering another bird's cache were more likely to move their cache to another site when they had been observed caching (compared to when they cached in private). On the other hand, naïve birds did not hide their caches in new locations (Emery and Clayton 2001). This suggests that individual scrub jays may be able to project their experience of pilfering caches onto other birds, and subsequently change their cache-protection strategy (Emery & Clayton 2004). Here I provided the nutcrackers with experience pilfering the caches of other birds, as well as experience having their own caches pilfered, to see how this experience might affect their caching and recovery behavior. If experience is important, we should expect an increase in cache-protection behavior (both increased caching in the hidden tray when observed and increased recovery from the in-view tray when caching had been observed) after experience.

Methods

The same birds and apparatus were used as in Experiment 1 and 2. The two cob-filled trays were located such that one was in-view and the other was behind an "L" shaped ¾" white melamine visual barrier (55cm wide x 20 cm long x 52 cm high) and was therefore hidden from the observer (Figure 16). An opaque white barrier curtain was added as a partition to the observer cage, so that the observer's location was restricted to

the in-view side of the cage. After each 15 minute caching session, the number of cached nuts was compared to determine if the nutcrackers prefer to cache in a hidden location when a conspecific is watching (but not when alone). The number of nuts (in-view or hidden trays) was also counted after 5 minute recovery sessions (24 hours after caching), and the proportion of nuts recovered to nuts cached was calculated (see general procedures).

After I completed the initial Visual Barrier tests, I gave the birds experience with pilfering the caches of the other birds, and having their own caches pilfered. Each bird received four daily sessions of pilfer experience, interspersed with four daily sessions of "non-pilfer" experience. For the pilfer-experience, the experimenter placed a single caching tray in the center of one side of the caching arena. The focal bird was placed in the arena with a bowl of 50 pine nuts, and given the opportunity to cache or eat for 15 min in the presence of a conspecific observer. Then the birds were removed to temporary transfer boxes and the bowl and any leftover (un-cached) pine nuts were removed. The observer and cacher were then switched so that the observer was placed into the caching arena, and the cacher was placed into the observer cage. Then while the cacher watched, the "pilferer" was allowed 5 min to search and either eat or re-cache the other bird's hidden pine nuts. The identity of the observer was randomized so that each focal bird was observed once by each of the other four birds, and each bird pilfered the other four birds' caches once. The location of the observer cage (left or right side of the caching arena) was pseudo-randomized. Both birds were then removed to their home cages. After a 4-6 hour retention period, the experimenter removed most of the remaining nuts (if there were any), leaving at least one, but no more than two nuts and some scattered broken

shells in and around the tray. The experimenter placed the cacher back into the arena for 5 min to search and eat or re-cache the remaining nut(s). Thus, during the recovery session, the cacher found many fewer nuts than it had hidden. The purpose of these sessions was to provide experience that an observing bird may have pilfered their cache (an inference was required).

Alternating with these "pilfer" sessions, every other day the birds were given a 15 min "non-pilfer" session (for a total of four sessions of this type). These sessions were identical to the pilfer sessions, except that the observer cage remained empty so that the focal bird cached in private. After the caching sessions, the experimenter left the nuts in the tray exactly as the cacher had placed them. After the 4-6 hour retention period, the cacher was placed back in the arena for 5 min, and allowed to recover (eat or re-cache) their nuts in private. The purpose of including this private caching training on alternating days was to prevent the caching behavior from extinguishing. After all of the pilfering experience training was complete, Experiment 3 (Visual Barrier) was duplicated in its entirety (4 observed trials for each bird with 4 recoveries plus 4 private trials with 4 recoveries) to see if the results changed due to the pilfering experience.

Analysis. As in Experiments 1 and 2, for the caching data, I used a general linear model (GLM), repeated measures ANOVA, with session, social situation (observed or private), and tray (hidden or in-view) as the variables. I used paired samples *t*-tests to compare the total number of nuts cached and recovered in private and when observed, and the total number of nuts cached in hidden or in-view trays (to test for a phobia or attraction to the barrier, or an overall preference or dislike of the in-view area). Next, I used paired samples *t*-tests to compare the number of nuts cached in four pairwise

comparisons: 1) hidden/observed *vs.* in-view/observed, 2) hidden/private *vs.* in-view/private, 3) hidden/observed *vs.* hidden/private, and 4) in-view/observed *vs.* in-view/private. For the recovery analysis, I used the same procedures as in Experiment 1 and 2. I examined the same pairwise comparisons as in the caching analysis (listed above), using the proportion of nuts recovered as the dependent variable.

To analyze the results post-pilfer experience, I duplicated the statistical analysis (caching and recovery) described above. Then, I conducted an analysis to compare the birds' behavior between before and after the pilfering experience, using two-tailed paired *t*-tests, with Bonferroni corrections to compare conditions. Since I did not find any significant differences in caching or recovery, before and after the pilfer experience, I combined the before and after data to provide additional power to detect changes in behavior (N=40, instead of N=20). I conducted the identical statistical analysis for the combined data as reported previously, except with a larger N.

Results and Discussion

Caching. Prior to pilfering experience, no significant effect was detected for session ($F_{3,12} = 0.96$, $P = 0.44$), tray ($F_{1,4} = 0.55$, $P = 0.10$), social situation ($F_{1,4} = 0.02$, $P = 0.88$), session x social situation ($F_{3,12} = 0.98$, $P = 0.44$), session x tray ($F_{3,12} = 0.94$, $P = 0.45$), social situation x tray ($F_{1,4} = 3.29$, $P = 0.14$) or session x social situation x tray ($F_{3.12} = 2.52$, $P = 0.11$).

The nutcrackers cached more nuts in the hidden/observed condition (median = 8.5, IQR = 14.5) than they cached in the in-view/observed (median = 5.5, IQR = 8.5); however this difference was not significant (N = 20, $t_{19} = 1.54$, $\alpha_{obt} = 0.01$, $P = 0.14$; Figure 17 left panel). They also cached fewer nuts in the in-view/observed condition

(median = 5.5, IQR = 8.5), than in the in-view/private condition (median = 8, IQR = 12.5), but once again this difference is not significant (N = 20, t_{19} = -1.68, α_{obt} = 0.01, P = 0.11; Figure 17 left panel). The comparisons of hidden/private *vs.* in-view/private and hidden/observed *vs.* hidden/private were also not significant (all Ps > 0.05). There was no significant difference between the total number of nuts cached while observed (total of hidden and in-view trays, N = 40) and the total number of nuts cached in private (N = 40), or between the total number of nuts cached in hidden trays (total of observed and private, N = 40) and the total number of nuts cached in the in-view trays (N = 40) (Ps > 0.05).

After pilfering experience, the birds demonstrated a similar pattern of behavior as before experience. No significant effect was detected for session ($F_{3, 12}$ = 0.51, P = 0.69), tray ($F_{1, 4}$ = 1.28, P = 0.24), social situation ($F_{1, 4}$ = 3.55, P = 0.13), session x social situation ($F_{3, 12}$ = 0.35, P = 0.79), session x tray ($F_{3, 12}$ = 2.29, P = 0.13), social situation x tray ($F_{1, 4}$ = 2.41, P = 0.20), or session x social situation x tray ($F_{3.12}$ = 0.62, P = 0.61).

Just as they did before pilfer-experience, after experience the nutcrackers cached more nuts in the hidden/observed condition (median = 6.0, IQR = 12.0) than in the in-view/observed condition (median = 4.0, IQR = 10.8); however this difference was again not significant (N = 20, t_{19}= 0.31, α_{obt} = 0.01, P = 0.76; Figure 17 middle panel). Fewer nuts were cached in the in-view/observed condition (median = 4.0, IQR = 10.8), than in the in-view/private condition (median = 10.0, IQR = 8.5), but this difference was not significant (N = 20, t_{19}= -1.71, α_{obt} = 0.01, P = 0.09; Figure 17 middle panel). The only difference that I detected is that after pilfering experience, when the nutcrackers cached in private, they cached significantly fewer nuts in the hidden tray (median = 5.0, IQR =

8.5) than the in-view tray (median = 10.0, IQR = 8.5) (N= 20, t_{19} = -2.81, α_{obt} = 0.01, P = 0.01; Figure 17 middle panel). All other pairwise comparisons were not significant (all Ps > 0.05). When I compared the results from before and after pilfering experience, I did not detect any significant differences in number of nuts cached between any comparisons (all Ps > 0.05).

When I combined the data from before and after pilfering experience I again found a similar pattern of behavior as I saw both before and after pilfering experience. However, combining the data from before and after pilfering experience allowed me to detect a significant interaction of social situation x tray ($F_{1,4}$ = 6.34, P = 0.03). There were still no significant effects for session ($F_{3,27}$ = 0.87, P = 0.46), tray ($F_{1,9}$ = 0.14, P = 0.72), social situation ($F_{1,9}$ = 0.81, P = 0.39), session x social situation ($F_{3,27}$ = 0.45, P = 0.72), session x tray ($F_{3,27}$ = 2.23, P = 0.11), or session x social situation x tray ($F_{3.27}$ = 1.07, P = 0.38).

For the pairwise comparisons, the major difference using the combined data is that I was now able to detect that the nutcrackers cached significantly fewer nuts in the in-view/observed condition (median = 6.5, IQR = 8.5), than they cached in the in-view/private condition (median = 10.2, IQR = 11.5) (N = 40, t_{39} = -2.59, α_{obt} = 0.01, P = 0.01; Figure 17 right panel). They also cached more nuts in the hidden/observed condition (median = 9.0, IQR = 12) than in the in-view/observed condition (median = 6.5, IQR = 8.5); however this difference was not significant (N = 40, t_{39}= 1.34, α_{obt} = 0.01, P = 0.19; Figure 17 right panel). The birds also cached more nuts in the hidden/observed condition (median = 9.0, IQR = 12) than in the hidden/private condition (median = 6.7, IQR = 8.8), but again this difference is not significant (N = 40, t_{39} = 1.63,

$\alpha_{obt} = 0.01$, $P = 0.11$; Figure 17 right panel).

The cache-protection behavior seen in the current study in the asocial nutcrackers is similar to the behavior of more social scrub jays. Like scrub jays (Dally et al 2005a), the nutcrackers showed a significant decrease in caching in the in-view tray when they were observed. The nutcrackers showed a tendency to increase caching in the hidden tray when they were observed caching, although the differences never reached significance. On the other hand, the relatively social scrub jays demonstrated a significant increase in caching in the hidden tray when caching was observed (Dally et al. 2005a). It is not clear why the nutcrackers did not cache significantly more nuts in the hidden tray when they were observed. I initially thought they might have a phobia of the barrier, and this might counterbalance any tendency they might have had to cache more nuts in the hidden tray. However, the fact that overall they did not cache differently in the hidden versus the in-view tray does not support this idea (hidden median =15.5, in-view median = 16.0). If the birds did have a dislike of the barrier, then the fact that they cached more nuts in the hidden area (observed condition) in spite of this fear is even more remarkable. Unlike scrub jays, the nutcrackers did not exhibit an increase in caching (scrub jays showed an non-significant increase in caching when observed, Dally et al. 2005a), nor did they suppress caching.

Recovery. Prior to pilfering experience, there was a significant effect of tray ($F_{1,4} = 25.51$, $P < 0.01$) and social situation x tray ($F_{1,4} = 25.52$, $P < 0.01$), but no effect of session ($F_{3,12} = 1.43$, $P = 0.28$), social situation ($F_{1,4} = 3.36$, $P = 0.14$), session x social situation ($F_{3,12} = 1.91$, $P = 0.18$), session x tray ($F_{3,12} = 1.30$, $P = 0.32$), social situation x tray ($F_{1,4} = 0.01$, $P = 0.97$) or session x social situation x tray ($F_{3.12} = 1.85$, P =

0.19).

When the nutcrackers had been observed making caches they later recovered a significantly larger proportion of nuts from the in-view tray (median = 100%, IQR = 58.33%) than they recovered from the hidden tray (median = 54.2%, IQR = 77.5%) (N = 20, t_{19} = -3.29, α_{obt} = 0.01, $P < 0.01$, Figure 18 left panel). The birds also recovered a larger proportion of nuts from the in-view tray when they had been observed caching (median = 100%, IQR = 0%), than they recovered from the in-view tray when they had cached in private (median = 50%, IQR = 0%) (N = 20, t_{19} = 0.93, α_{obt} = 0.01, $P = 0.37$; Figure 18 left panel), but this was not a significant difference.

In total, there was no difference in mean proportion of nuts recovered when caching had been observed (total of hidden and in view-trays, median = 68.8%, IQR = 65.2%) than when caching had been private (median = 27.2%, IQR = 27.8%) (paired samples *t*-test, N = 20, t_{19} = 1.45, α_{obt} = 0.03, $P = 0.18$). However, the nutcrackers recovered a significantly larger proportion of nuts from in-view trays (total of observed and private, median = 54.4%, IQR = 50.4%) than from the hidden trays (median = 34.3%, IQR = 58.8%) (N = 20, T_{19} = -3.61, α_{obt} = 0.03, $P < 0.01$).

Again, after pilfering experience, the birds exhibited a similar pattern of behavior as they did before pilfering experience. However, now I was unable to detect any significant effects for session ($F_{3, 12} = 0.90$, $P = 0.47$), tray ($F_{1, 4} = 1.20$, $P = 0.34$), social situation ($F_{1, 4} = 2.80$ $P = 0.17$), session x social situation ($F_{3, 12} = 0.83$, $P = 0.50$), session x tray ($F_{3, 12} = 1.70$, $P = 0.22$), social situation x tray ($F_{1, 4} = 2.10$, $P = 0.22$), or session x social situation x tray ($F_{3.12} = 1.92$, P = 0.18).

The main difference from the pairwise comparisons is that when the nutcrackers

had been observed caching (just as before pilfering), they again recovered a larger proportion of nuts from the in-view tray (median = 91.7%, IQR = 74.4%), than they recovered from the hidden tray (median = 32.6%, IQR = 80.1%), but this difference was no longer significant (N = 20, t_{19} = -1.41, α_{obt} = 0.01, P = 0.18, Figure 18 middle panel). They also recovered a larger proportion of nuts from the in-view tray when they were previously observed caching (median = 91.7%, IQR = 74.4%), than they recovered from the in-view tray when they had cached in private (median = 50%, IQR = 65%); but this difference was not still not significant (N = 20, t_{19} = 1.81, α_{obt} = 0.01, P = 0.09; Figure 18 middle panel). When the results were compared before and after pilfering experience, I found no significant difference in proportion of nuts recovered between any comparison before and after pilfering (all Ps > 0.05).

When the data from before and after pilfering experience were combined, the results showed the exact pattern as before pilfering experience. I again detected a significant effect of situation x tray ($F_{1, 4}$ = 6.38, P = 0.03). No significant effect was detected for session ($F_{3, 27}$ = 0.76, P = 0.53), tray ($F_{1, 4}$ = 6.38, P = 0.03), social situation ($F_{1, 9}$ = 6.44, P = 0.03), session x social situation ($F_{3, 27}$ = 0.63, P = 0.60), session x tray ($F_{3, 27}$ = 0.40, P = 0.76), or session x social situation x tray ($F_{3,27}$ = 2.93, P = 0.08).

Just as before experience, when the nutcrackers had been observed caching, they recovered a significantly larger proportion of nuts from the in-view tray (median = 100%, IQR = 62.2%) than they did from the hidden tray (median = 41.1%, IQR = 73.5%) (N = 40, t_{39} = -2.53, α_{obt} = 0.01, P = 0.01; Figure 18 right panel). The combined data indicate (just as before experience) a larger proportion of nuts recovered from the in-view tray when the birds were previously observed caching (median = 100%, IQR = 62.2%), than

in the in-view tray when they had cached in private (median = 50%, IQR = 78.8%); this difference approached but still did not quite reach significance (N = 40, $t_{39} = 2.02$, $\alpha_{obt} = 0.01$, $P = 0.050$; Figure 18 right panel).

With regard to recovery, the asocial nutcrackers showed sensitivity to the observer, by increasing recovery from the in-view tray when caching had been observed. The nutcrackers recovered a large percentage (overall ~ 45%) of nuts that they cached. Overall the nutcrackers recovered more nuts when they had cached in the presence of an observer than they did when they had cached in private (but this was not a significant difference). Interestingly, overall they recovered significantly more nuts from the in-view trays than from the hidden trays (both observed and in private). At first glance this looks like either an indication of a phobia of caching behind the barrier, or a preference to cache in the open. Upon further inspection though, this difference stems from the fact that they recovered significantly more nuts from the in-view tray, but only when caching had been observed (not when caching was in private). This is exactly the pattern I would expect to see if the nutcrackers are sensitive to an observer and alter their behavior accordingly. I had hoped to directly compare of recovery behavior between nutcrackers and scrub jays. However, as in the Experiment 2 (Effect of Lighting) due to low numbers of nuts recovered by the scrub jays (Dally et al 2005a), a comparison of those data was not possible. Therefore, it is not clear whether scrub jays (like nutcrackers) alter their recovery behavior when observed making caches.

Effect of experience. The experience of pilfering did not seem to have a large impact on cache-protection behavior, since the pattern of caching behavior exhibited by the nutcrackers was similar both before and after pilfering experience. In the observed

condition, the nutcrackers again showed a tendency to protect their caches by caching less in the in-view tray than the hidden tray when observed (however, like before the difference it did not reach significance), but not in private. The only difference in caching behavior from before and after pilfer experience is that the nutcrackers actually seemed to slightly decrease caching in the hidden tray after pilfering experience, although this difference was not significant. Of course, it is possible that the pilfering experience I provided was insufficient to induce a dramatic increase in cache-protection behavior. If the nutcrackers were given more experience (perhaps by providing additional sessions of pilfering and being pilfered) they may have shown an increase in caching in the hidden tray and recovery from the in-view tray when observed. The analysis of the combined data from before and after pilfer experience again revealed an identical pattern of results for caching as in both before and after pilfer experience. When the data were combined, the main difference is that I was now able to detect a significant decrease in caching in the in-view tray when the birds were observed (as compared to when caching in private). Thus, in general, the nutcrackers show flexible cache-protection behavior in the presence of a conspecific observer.

The pattern of recovery behavior (like caching behavior) exhibited by the nutcrackers after pilfering experience also suggests a minimal effect of experience. The birds' behavior was essentially identical before and after experience with pilfering. Again, the nutcrackers recovered the largest proportion of nuts from the in-view tray when they were observed (more than both hidden/observed and in-view/private). The only difference in recovery behavior from before and after pilfer experience is that although the nutcrackers again increased recovery from the in-view tray when caching

had been observed, after experience this was no longer significantly different than recovery from the hidden tray. Using the combined data I detected the same recovery behavior that I saw pre-pilfer experience; the nutcrackers recovered significantly more nuts from the in-view tray when observed.

Thus, the results of this experiment indicate that experience may not be necessary for the nutcrackers to demonstrate a pattern of behavior consistent with cache-protection. It is possible that sufficient experience with pilfering was acquired either before birds were captured, or from routine experience in the laboratory. However, the nutcrackers probably did not have an opportunity to learn about pilfering in the laboratory because their cages are spatially separated, the birds have no physical contact, and they are unable to access each other's food. Therefore, the results of this experiment may suggest that either 1) the tendency for the nutcrackers to increase caching in a hidden location when observed is innate, or 2) the nutcrackers in this study (which were wild-caught), may have learned about pilfering before capture, but this would have been many years before the current experiment. To distinguish between these two possibilities, naive birds could be tested. The major difference between nutcrackers and scrub jays (Dally et al. 2005a) is that scrub jays seem to increase cache-protection after having minimal experience with pilfering, while nutcrackers seem to demonstrate the same pattern of behavior before and after pilfer experience.

Experiment 4- Caching efficiency

It was my impression in Experiment 3 that when the nutcrackers were observed by a conspecific, they increased their level of activity in the vicinity of the in-view tray. It appeared that the birds increased digging in the cobs, repeatedly caching and un-caching

nuts in the in-view tray (and not in the hidden tray). If so, the nutcrackers may have been demonstrating a different form of cache-protection behavior, such as false-caching in the in-view tray, guarding their cache, or intimidating the observer. To examine these possibilities, and to quantify this perceived activity, I created two new variables to measure caching efficiency, "caching frequency" and "caching rate".

Methods

After the main Visual Barrier experiment was complete, I randomly selected eight of those 20 videos (I made sure to include at least one video from each of the five nutcrackers) from the observed condition, and eight videos from the private condition. First, to examine caching frequency, I watched the videos and scored the number of pecks made to each tray (number of times a bird's beak was inserted into the cobs in the in-view and hidden trays). Then to calculate caching frequency, I divided the number of nuts cached in a tray by the number of pecks to that tray (thus caching frequency = nuts/peck). Thus, if the birds cached with perfect efficiency, the ratio of nuts/peck would be 1/1 or 1 (one nut cached for every peck to the substrate). By this definition, a low score on caching rate would mean that the birds made a large number of pecks to the substrate without depositing many nuts, and could indicate false-caching.

Next, to examine caching rate, I watched all of the videos from the visual barrier experiment (N=20), and this time I scored the amount of time a bird spent (without regard to behavior) in two of the three sections of the arena (in-view and hidden areas, note: the third 'neutral' area was not scored) of the caching arena. Then, to calculate caching rate, I divided the number of nuts cached in that tray by the number of seconds spent in that section (thus caching rate = nuts/second). On this scale, a score of 1 would indicate that

the birds cached with perfect efficiency (one nut cached for every second spent in the vicinity of a tray). A low score on caching rate would mean that the birds spent a lot of time near a tray without caching in that tray, and might indicate either false-caching or cache-guarding behavior.

I conducted two-tailed paired *t*-tests to compare caching frequency and caching rate in observed *vs.* private conditions, and in hidden *vs.* in-view trays. Caching frequency and caching rate were also compared among these groups: hidden/observed *vs.* in-view/observed, hidden/private *vs.* in-view/private, hidden/observed *vs.* hidden/private, and in-view/observed *vs.* in-view/private. To maintain family-wise error rate, I used a Bonferroni correction, and α_{obt} are reported.

Results and Discussion

Number of pecks. In general, the birds made a large number of pecks to the substrate in the 15 minute sessions. When the birds were observed, they pecked significantly more in the in-view tray (Mean = 275.3, SE = 40.4) than the hidden tray (Mean = 35.6, SE = 10.3) (paired *t*-test, N = 8, $t_7 = 6.91$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 19 left panel). In the private condition, the birds also made significantly more pecks in the in-view tray (Mean = 234.9, SE = 50.3) than in the hidden tray (Mean = 54.4, SE = 15.5) (paired t-test, N = 8, $t_7 = 3.40$, $\alpha_{obt} = 0.01$, $P = 0.01$, Figure 19 left panel). There were no other significant pairwise differences (all Ps > 0.05).

In general, the nutcrackers pecked significantly more in the in-view trays (Mean = 253.7, SE = 31.1) than in the hidden trays (Mean = 46.5, SE = 45.5) (N = 16, $t_{15} = -6.40$, $\alpha_{obt} = 0.03$, $P < 0.01$). There was no difference in number of pecks when the nutcrackers were observed making caches (Mean = 156.4, SE = 38.6) than when they cached in

private (Mean = 144.6, SE = 34.5) (paired t-test, N = 16, $t_{15} = 0.10$, $\alpha_{obt} = 0.03$, $P = 0.93$).

Caching frequency. When they were observed caching, the birds cached significantly more nuts per peck in the hidden tray (mean = 0.32, SE = 0.10) than the in-view tray (Mean = 0.05, SE = 0.02) (paired t-test, N = 8, $t_7 = 2.88$, $\alpha_{obt} = 0.01$, $P = 0.01$; Figure 19 right panel). There were no other significant pairwise differences (all Ps > 0.05). In general, the nutcrackers cached significantly more nuts per peck in the hidden trays (Mean = 0.31, SE = 0.26) than they did in the in-view trays (Mean = 0.09, SE = 0.11) (N = 16, t_{15} =, $\alpha_{obt} = 0.03$, $P = 0.01$). There was no difference in number of nuts cached per peck when the nutcrackers were observed making caches (Mean = 0.19, SE = 0.06) than when they cached in private (Mean = 0.21, SE = 0.05) (paired t-test, N = 16, $t_{15} = -0.16$, $\alpha_{obt} = 0.03$, $P = 0.88$).

Time spent in vicinity of trays. When the birds were observed, they spent significantly more time near the in-view tray (Mean = 443.5, SE = 97.9) than near the hidden tray (Mean = 75.3, SE = 16.3) (paired t-test, N = 20, $t_{19} = -6.79$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 20 left panel). In the private condition, the birds also spent significantly more time near the in-view tray (Mean = 387.06, SE = 39.62) than the hidden tray (Mean = 97.0, SE = 21.28) than (paired t-test, N = 20, $t_{19} = 5.69$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 20, left panel). There were no other significant pairwise differences (all Ps > 0.05).

Overall, the nutcrackers spent significantly more time near the in-view trays (Mean = 416.76s, SE = 30.77) than they spent near the hidden trays (Mean = 85.58s, SE = 13.19) (N = 40, $t_{19} = -8.85$, $\alpha_{obt} = 0.03$, $P < 0.01$). There was no difference in the amount of time spent in the vicinity of the trays when the nutcrackers were observed making caches (Mean = 259.0s, SE = 38.21) than when they cached in private (Mean =

242.03s, SE = 33.05) (paired t-test, N = 40, $t_{39} = 0.35$, $\alpha_{obt} = 0.03$, $P = 0.73$).

Caching rate. In the observed condition, the birds cached significantly more nuts per second in the hidden tray (Mean = 0.19, SE = 0.04) than the in-view tray (Mean = 0.02, SE = 0.01) (paired t-test, N = 20, $t_{19} = 4.49$, $\alpha_{obt} = 0.01$, $P < 0.01$; Figure 20 right panel). In the private condition, the birds also cached more nuts per second in the hidden tray (Mean = 0.19, SE = 0.06) than the in-view tray (Mean = 0.04, SE = 0.01), but this difference was not significant (N = 20, $t_{19} = 2.28$, $\alpha_{obt} = 0.01$, $P = 0.04$; Figure 20 right panel). There were no other significant pairwise differences (all Ps > 0.05).

In general, the nutcrackers cached significantly more nuts per second in the hidden trays (Mean = 0.19, SE = 0.34) than they did in the in-view trays (Mean = 0.10,SE = 0.03) (N = 40, $t_{39} = 3.71$, $\alpha_{obt} = 0.03$, $P < 0.01$); but there was no difference in number of nuts cached per second when the nutcrackers were observed making caches (Mean = 0.10, SE = 0.02) than there were when they cached in private (Mean = 0.12, SE = 0.03) (paired t-test, N = 40, $t_{39} = -0.56$, $\alpha_{obt} = 0.03$, $P = 0.58$).

When they were observed making caches, the nutcrackers cached with more efficiency in the hidden trays, showing both a significantly higher caching frequency (more nuts per peck) and a significantly higher caching rate (more nuts per second) in the hidden trays. The nutcrackers pecked more in the in-view trays both when they were observed and when they were alone. These results may be interpreted in one of two ways, either they birds did not like the barrier, or they preferred to be out in the open. However closer analysis examining the number of nuts the birds cached per peck to the substrate revealed that they only cached significantly more nuts in the hidden tray when they were observed caching (but not in the private condition). Thus, it may be likely that the

nutcrackers were exhibiting cache protection (guarding or intimidation behavior) or even false-caching (deceptive behavior), by pecking a great deal without caching in the in-view trays.

The data for time spent in the vicinity of the trays and caching rate show a similar pattern. The nutcrackers spent more time near the in-view trays than the hidden trays during both private and observed trials. At first glance it seems that the nutcrackers may have disliked the barrier, or preferred being near the open tray. However, analysis of caching rate (number of nuts cached per second) indicates that the nutcrackers cached significantly more nuts per second in the hidden tray, but only when they were observed. This strongly suggests that they are sensitive to the presence of the observer, and that they alter their behavior when observed by caching more efficiently in the hidden tray when observed. These results are different than those obtained for scrub jays, which spent approximately the same amount of time in the hidden and in-view areas, even though they cached more in the hidden tray when observed (Dally et al. 2005a). Dally's group they also found that scrub jays increase caching rate in the hidden tray when they are observed (Dally et al, 2005a). Thus, the relatively asocial nutcrackers behave similarly to the more social scrub jay, in terms of altering caching rate according to social situation (observed versus private).

Considering the analysis of caching frequency (the amount of time spent in each area) in conjunction with the analysis of caching rate (the number of nuts deposited in each area), I can gain a clearer picture of what the birds are actually doing. Taking these results together (increased caching frequency and increased caching rate in the hidden tray when observed, coupled with a large amount of time spent pecking without caching

at the in-view tray when observed), I posit that the nutcrackers may have been exhibiting false-caching in the in-view tray (observed condition only). If so, this could indicate an intentionally deceptive behavior.

Experiment 5- Control for Social Interactions

Here I was interested in distinguishing between cache-protection and (territorial-type) aggression directed towards a conspecific. In Experiment 3 (Visual Barrier), the nutcrackers spent the vast amount of time near the in-view tray (in the observed condition), and very little time near the hidden tray or in the neutral area (farther away from the other bird but still in view). The results from that experiment suggest that the birds may have been engaging in a form of cache-guarding behavior or perhaps even false-caching. In this experiment, I was interested in determining if the birds would demonstrate the same behavior (staying near the observer) in the absence of food. If they did, it would suggest that the birds were simply exhibiting aggression (territoriality), rather than cache-guarding. The nutcrackers used in this study typically exhibit hostility toward each other (personal observation), even though they have lived together for a long time, in close proximity. In the laboratory, they must be kept separated or they will attack one another. When one bird comes too close to another's cage, the resident will try to bite and fly at the "invader" violently (personal observation). Bednekoff and Balda (1997) commented that the stress of seeing the "aggressive actions" of the caching nutcrackers may have contributed to their difficulty finding others' caches. In the wild, although individual behavior varies, nutcrackers often aggressively defend their territories from conspecifics (Lorenz 2008). These are bold birds, known to readily approach humans for food at campsites and parks, and (anecdotally) sometimes chase large mammals away

from their nests. The other possibility is that in Experiment 3, the nutcrackers were guarding their food from the other bird, perhaps by intimidation. If that were the case, then removal of the food might result in the birds spending less time near the observer. Therefore, to tease apart these possibilities (territoriality versus food-guarding), I removed the food and repeated the visual barrier experiment. I then compared the amount of time spent in each section of the arena in both the presence and in the absence of food. I also hoped to answer additional questions such as: do the nutcrackers generally prefer to keep a conspecific in-view or do they prefer to hide from the other bird? I also used the data to examine whether the individual identity of birds in a pairing had an effect on the amount of time spent close or far away from an observer (i.e. were there any pair combinations that were especially aggressive or non-aggressive).

Methods

The same birds and apparatus were used as in Experiment 1, 2 and 3 (with the exceptions that the food bowl was not used, and I used masking tape to demarcate the floor of the caching arena into three sections. The sections were delineated as follows: 1) in-view area- to one side of the barrier and close to the observing bird, 2) hidden area- also close but visually obscured by the barrier, and 3) neutral area, the large area which is farther away and is mostly visible to the observer (Figure 21). The location of the visual barrier was counterbalanced between the left and right side of the arena. Each individual bird participated in two daily trials, one trial as the focal bird, and one trial as the observer. The pairings were counterbalanced, such that each bird was paired only once with every other bird as an observer, over a period of 5 days. During each trial, a focal bird was placed in the caching arena, and another bird was placed in the observer cage

(restricted to the in-view side by the partition, see previous description). I videotaped the interaction for 20 min. Later, I watched the first 15 min of each video, and used a stopwatch to score the amount of time (in secs) that the focal bird spent in each of the three sections. Because the neutral area is much larger than the other two areas, I adjusted the time spent in the hidden and in-view sections accordingly. I then re-watched the 20 (previously recorded) videos from the original visual barrier experiment (caching-observed condition, pre-pilfer experience). For each video, I marked a line on the computer screen with removable tape to delineate the same three sections (as in Figure 21). I then scored the amount of time spent in each of the three sections. I again adjusted the amount of time spent in each section for the relative proportion of the total area of the arena.

Analysis. Initially I conducted an ANOVA comparing pairs of birds (each pair was tested twice, once with bird A as the focal bird, and once with bird B as the focal bird) to determine if there was an effect of the identity of birds in a pairing (for social interactions and caching interactions). Then I used paired *t*-tests (see previous) to compare the amount of time spent in each section during the social interactions (food absent). I compared the amount of time spent (adjusted for relative area) between in-view *vs.* hidden, neutral *vs.* hidden, and in-view *vs.* neutral. Second, I repeated this analysis for the caching (observed) sessions (with food present). Next, the amount of time spent in each of the three sections in the social interactions was compared to the amount of time spent in each of the three sections during caching sessions, using paired t-tests to make the following comparisons: in-view/social *vs.* in-view/caching, hidden/social *vs.* hidden/caching, and neutral/social *vs.* neutral/caching.

Results and Discussion

No Food- Social interactions. When food was absent, the nutcrackers spent significantly more time in the in-view area (Mean = 1018.0 s/sq in (adj), SE = 276.47) than the hidden area (Mean = 105.0 s/sq in (adj), SE = 30.86) (N = 20, $t_{19} = 3.17$, $\alpha_{obt} = 0.02$, $P < 0.01$; Figure 22 left panel). The birds also spent significantly more time near in the neutral area (Mean = 892.0 s/sq in (adj), SE = 74.96) than the hidden area (N = 20, $t_{19} = -10.54$, $\alpha_{obt} = 0.02$, $P < 0.01$; Figure 22 left panel). There was no significant effect of pairing (ANOVA $F_{9, 10} = 0.50$, $P = 0.84$), thus there were no differences in the amount of time spent in the three sections that differed for any particular pairs of birds.

Food- Caching. When food was present in the arena, the nutcrackers again spent significantly more time in the in-view area (Mean = 1586.0 s/sq in (adj), SE = 166.17), than the hidden area (Mean = 269.0 s/sq in (adj), SE = 58.42) (N = 20, $t_{19} = 6.79$, $\alpha_{obt} = 0.017$, $P < 0.01$; Figure 22 right panel). However now, the birds also spent significantly more time near the in-view tray than in the neutral area (Mean = 417.0 s/sq in (adj), SE = 44.87) (N = 20, $t_{19} = 5.68$, $\alpha_{obt} = 0.017$, $P < 0.01$; Figure 22 right panel). Again there was no significant effect of pairing (ANOVA $F_{9, 10} = 0.59$, $P = 0.78$).

Comparison of Behavior With and Without Food. There were several significant differences in behavior in the presence and absence of food. First, the birds spent significantly more time in the in-view area when food was present (Mean = 1586.0 s/sq in (adj), SE = 166.17) than they did in the in-view area when food was absent (Mean = 1018.0 s/sq in (adj) (N = 20, $t_{19} = 3.24$, $\alpha_{obt} = 0.02$, $P = 0.01$; Figure 22 both panels). The birds also spent significantly more time in the hidden area when food was present (Mean = 269.0 s/sq in (adj), SE = 58.42) than they did in the hidden area when food was absent

(Mean = 105.0 s/sq in (adj), SE = 30.86) (N = 20, t_{19} = 3.40, α_{obt} = 0.02, P = 0.01; Figure 22). Lastly, they spent significantly less time in the neutral area when food was present (Mean = 417.0 s/sq in (adj), SE = 44.87), than when food was absent (Mean = 892.0 s/sq in (adj), SE = 74.96) (N = 20, t_{19} = -6.94, α_{obt} = 0.02, $P < 0.01$; Figure 22).

The results from this experiment clearly indicate that the nutcrackers spent significantly more time close to the observer when food was present than they did when food was absent. This strongly suggests that the nutcrackers were exhibiting a form of food-guarding behavior. Combined with the results from the caching frequency experiment (Experiment 4), in which the nutcrackers pecked intensely without caching in the in-view tray when observed, it seems that the nutcrackers may have been exhibiting false-caching, a strategy which might be used to intentionally deceive the observer (potential pilferer). It is true that, whether food is present or absent, the nutcrackers spent a lot of time in the in-view area close to the observing birds. These results suggests that the birds spent a good deal of time engaging in social interactions when food is absent, and that during caching even more time is spent engaging in cache-related behaviors. The birds also spent significantly more time in the hidden area when food was present than they did when there was no food available. This is likely because they were spending time caching nuts in the hidden area. In the absence of food, there was no need to spend time in the hidden area, unless the birds wanted to hide from the observer. Wild nutcrackers are territorially aggressively (Lorenz 2008). Thus, given the aggressive nature of these birds, it is not surprising that they did not hide from a conspecific. The birds spent significantly less time in the neutral area when food was present than when food was absent. This can be explained by the fact that when food was present, the birds

spent their time either caching in the hidden tray or guarding food (or false-caching) in the in-view tray. It is also interesting to note that these patterns (spending time near the observer when food was present, etc.) were independent of the identities of the birds that were paired in the interactions (with and without food). Therefore, it would seem that the propensity of the birds to cache in the hidden zone when observed during testing is independent of social relationships.

Experiment 6- Comparison of the number of nuts cached and recovered by nutcrackers and scrub jays

Since I replicated the experiments with scrub jays closely, a comparison of the overall number of nuts cached and recovered by nutcrackers and scrub jays is possible. The most comparable study is that of Dally and colleagues (2004), in which scrub jays were given a bowl a 50 of pine nuts, and a 15 minute period in which to cache (or eat) them. I used the same procedures, except that the caching arena was made larger for the larger nutcrackers (see general procedures/apparatus).

Methods

Using the data from Experiment 2 (Effect of Lighting) and data from Dally's (2004) experiment, I compared the number of pine nuts (out of 50) cached in a 15 minute period and the proportion of pine nuts recovered in a 5 minute period between nutcrackers and scrub jays (no statistical analyses were conducted).

Results and Discussion

The nutcrackers cached more nuts than scrub jays (in Dally et al. 2004) in the same 15 minute test interval. The nutcrackers cached a median of 24.5 nuts (total cached in sun and shade) when observed (IQR = 18.5) compared to the scrub jays, which cached

a median of only 2 nuts when observed (IQR = 5.0). The nutcrackers cached a median of 22.5 nuts in private (IQR = 17.8), compared to the scrub jays, which cached a median of only 3.5 nuts in private (IQR = 12.0) (Figure 23).

The nutcrackers also recovered a larger proportion (not shown) of the nuts that they had cached than the scrub jays recovered in the same 5 minute interval (from Dally et al 2004). The nutcrackers recovered a median of 36.5% (IQR = 64.59%) of nuts when they had been observed making caches, compared to the scrub jays which recovered a median of 0% of nuts when observed (IQR = 61.0%). The nutcrackers recovered a median of 37.5 % (IQR = 63.8%) of nuts when they had cached in private, and the scrub jays recovered a median 0% (IQR = 7.0%) of nuts when they cached in private.

The overall number of nuts cached and recovered by nutcrackers in the current study seems to generally concur with results from a similar study with nutcrackers (Clary and Kelly 2011); even though the nutcrackers in that study were given more time to cache (1 hour as opposed to 15 minutes) and recover (15 minutes as opposed to 5 minutes). It does not seem surprising the nutcrackers cache and recover more than scrub jays. In the harsh environment that they inhabit, nutcrackers probably rely more heavily on their caches than scrub jays rely on any single food resource. Therefore, nutcrackers may be hardwired to recover a large proportion of food that they have cached. This might also be a failsafe; in natural conditions it is possible that observers could be unseen. Thus, one possible strategy a cacher can use is to relocate food that was seen by an observer. On the other hand, if a cacher is unsure of who has seen the caching event, the cacher could simply relocate most of the food that was cached. This would serve to confuse both seen and unseen observers. This behavior, of course, would theoretically utilize more

energy than relocating only food which was surely seen. Therefore, in order for this strategy to be profitable, the risk of being pilfered by unseen conspecifics (and heterospecifics) would be expected to be very high. This hypothesis remains to be tested.

Another reason that nutcrackers might cache more food than scrub jays is that they are larger in size than scrub jays. Although the average overall length including the tail is about the same in the two species (scrubs jays have a relatively long tail), the nutcracker has a larger average wingspan (~15%) and a larger average mass (~35%). Furthermore, Clark's nutcrackers have a sublingual pouch that they use to transport up to 82 whitebark pine seeds (*Pinus albicaulis*, Lanner 1996). In the family Corvidae, the sublingual pouch is unique to the two species in the genus *Nucifraga,* the Clark's nutcracker and the Eurasian nutcracker, *Nucifraga caryocatactes* (Raby and Clayton 2010). The possession of this pouch may explain why nutcrackers may cache and recover more than scrub jays (ease of handling, optimal foraging), which must carry seeds in their mouths.

General Discussion

The caching behavior exhibited by the nutcrackers in this study indicates that they are sensitive to the presence of a conspecific observer, and that they use several different strategies to protect their caches. For example, when the nutcrackers were given a choice to cache in a cob-filled tray either near an observer or far away, the nutcrackers chose to cache farther way. When they cached in private however, they did not show this preference. This is very similar to the behavior of scrub jays (Dally 2005a), which also cached more in a far location in the presence of an observer. The nutcrackers in the current study also significantly reduced caching in a tray that was in plain view of the

observer (compared to a visually hidden tray), but they did not reduce caching in the same tray when they cached in private (with an empty cage). The nutcrackers also showed a tendency to cache more nuts in the tray that was hidden behind a visual barrier than they did in a tray that was in plain view of the observer (although not significantly more). This is again similar to the pattern of behavior demonstrated by scrub jays (Dally et al 2005a), which also showed a (non-significant) propensity to cache more nuts in a hidden tray than an in-view tray when observed.

Another way an animal can protect their food resource is to hide food in difficult-to-see or poorly lit locations. However, when they were given a choice between shady and sunny locations, the nutcrackers did not preferentially cache in the shady location when they were observed. This is different than the behavior seen in scrub jays, which preferred to cache in a shady location (Dally et al 2004). It is not clear why the nutcrackers differed from scrub jays in only this cache-protection strategy. Perhaps the difference in illumination between the two studies could account for the lack of sensitivity in the nutcrackers. I used a 60 w bulb, while Dally's group did not indicate the bulb intensity they used (however the ratio of luminance between the two sides in that study was 4:1). It is doubtful that the nutcrackers were unable to distinguish between the illumination of the two sides; to the human eye it was clearly much darker on the shady side of the arena. It is possible that the caching nutcrackers had no problem seeing the tray in the shady area themselves; therefore they may not have considered hiding food in the shade a protective strategy. This could explain why they cached in both shady and sunny trays, both when observed and in private.

I also looked at several additional measures of cache-protection, to further

examine how nutcrackers might change their behavior with regard to food storing when a conspecific is watching. To protect food stores from potential pilferers, another strategy that an animal could use is to increase the efficiency of their caching activity in hidden locations. This could be accomplished either by increasing either the frequency or the rate of caching. First I examined caching frequency by calculating the number of nuts deposited per peck in each of several conditions (a novel measure). The nutcrackers exhibited a high caching frequency (nuts/peck) in the hidden tray (both when caching was observed and in private), however this frequency was only significantly different than the in-view tray when caching was observed. In other words, when the birds were observed making caches, they cached a lot of nuts in the hidden tray, and pecked more without depositing nuts in the in-view tray. This behavior could indicate that the nutcrackers may have been actively guarding the area against a possible pilferer through the use of intimidation; or they may have been using the activity as a distraction (false-caching) in an attempt to confuse the observer. I cannot compare this finding with other corvids, because I am not aware of any other studies that have examined caching frequency or have documented this behavior in birds.

I also examined caching rate, calculated as the number of pecks in the substrate per second. The nutcrackers exhibited a high caching rate (nuts/second) in the hidden tray (both when caching was observed and in private), however this was only significantly different than the in-view tray when caching was observed. In other words, when the birds were observed making caches, they cached nuts quickly in the hidden tray and slowly in the in-view tray. This again suggests that the birds spent more time in-view, directing activity toward the in-view tray without caching there (observed only). This

behavior is consistent with scrub jays, which also increased the rate of caching in a hidden tray when observed (Dally et al. 2005a). Further evidence that the nutcrackers were engaging in some sort of guarding or deceptive behavior comes from my investigation of the amount of time that nutcrackers spent in three regions of the caching arena (in-view, hidden, and neutral areas), with and without food available. When an observer was present, the nutcrackers spent more time close to the observer near the in-view tray, compared with when there was no food in the arena. However, the data indicate that this time was not spent caching nuts in-view. Taken together, these results strongly suggest that the nutcrackers were likely either guarding their food, trying to intimidate or confuse the potential pilferer, or making false-caches.

Interestingly, for nutcrackers, experience did not have a large impact on caching behavior; they showed a similar pattern of caching both before and after they were given experience pilfering the caches of others and having their own caches pilfered. My results concur with another study aimed at examining pilfering experience in nutcrackers. Clary and Kelly (2011) found no significant difference in number of nuts cached between experienced and naïve wild-caught nutcrackers. Scrub jays, on the other hand, seem to increase cache protection after pilfering experience (Emery and Clayton 2001).

Because I used the same procedures, I am able to make a direct comparison of cache suppression or increased caching between scrub jays and nutcrackers. The nutcrackers in this study did not exhibit cache suppression (or increase) in the presence of an observer, in any of the experiments or conditions that I tested, even after pilfering experience. This differs from the result obtained by Clary and Kelly (2001). Using a slightly different paradigm, they trained nutcrackers that food cached in a tray that was

near to an observer would be pilfered (unavailable during recovery). The nutcrackers in that study suppressed caching over successive trials when they were observed and during the private caching sessions. This reduction was not seen when a "dummy" bird (coke bottle) was used as the observer. Importantly, in their study, in the private condition a conspecific was present but not visible; thus the birds were not acoustically isolated from one another. This suggests that the auditory presence of the conspecific may have been sufficient to promote cache-protection. It is not clear why the nutcrackers in the current study did not reduce caching in the presence of an observer. Perhaps differences in learning history (birds have been together longer), or differences in the training and testing paradigm could account for the lack of cache suppression in these nutcrackers. My results also differ from scrub jays, which showed an increase in caching when observed compared to in private (Dally et al. 2005a). Dally and colleagues suggest that increasing caching is a compensatory tactic, used in conjunction with the distance strategy. Although it is an energetically costly strategy, increased caching while observed has been documented in other species (Bossema 1979; Emery et al. 2004); it may be used when other strategies are not possible. In the current study, the nutcrackers may have preferred to use other tactics rather than increasing or suppressing caching when observed, such as caching in the far tray, along with intimidation and false-caching in the near-tray.

In general, the nutcrackers cached more nuts than scrub jays. I consistently found (across experiments and conditions) that nutcrackers cached approximately 20-40% more nuts than scrub jays in the same 15 minute period. Nutcrackers may cache more than scrub jays for several reasons. First they are a larger bird than scrub jays, both in wingspan (~15% larger) and average mass (~35% larger). Second, the sublingual pouch

in nutcrackers may make caching more efficient (easier to transport and handle large number of nuts). Lastly, nutcrackers live in a harsher climate and are food specialists. Their heavy reliance on their food stores could explain how the ability to cache large numbers of nuts may have evolved.

Sensitivity to the presence of an observer can also be exhibited by the choices an animal makes during recovery of food that it had previously cached. Just as with caching behavior, the nutcrackers' behavior during recovery also indicates that they are sensitive to the presence of a conspecific observer. In the Experiment 3 (Visual Barrier), the nutcrackers recovered more nuts from the in-view tray when they had been observed caching than they recovered from the hidden tray (or from the in-view tray when they had caching in private). My results are consistent with Clary and Kelly (2011), in which nutcrackers also recovered a significantly higher proportion of seeds when they had been observed caching than when they had cached in private or in front of a dummy. Again, for the nutcrackers, experience with pilfering did not seem to have a large impact; they showed the same pattern of behavior with regard to recovery both before and after the pilfering experience. I cannot compare the nutcrackers performance to that of more social scrub jays (Dally et al 2005a), because the scrub jays did not recover enough nuts for analysis.

In all experiments and conditions, the nutcrackers recovered a large proportion of nuts they had cached (~40-70%); and in many cases they recovered 100% of the hidden food. Nutcrackers recovered approximately 10-50% more nuts than scrub jays in the same 5 minute period. My results are also consistent with those from Clary and Kelly (2011); in which nutcrackers recovered ~68% of nuts they cached in a 15 minute period

(a bit more than the nutcrackers were able to recover in a 5 minute recovery period). Just as with caching, nutcrackers may recover more than scrub jays for several reasons. Being of a larger size and possessing a sublingual pouch may facilitate efficient recovery; and food specialization and living in a harsh environment may have driven the need for efficient recovery behavior.

My results suggest that sociality may not be the sole predictor of social intelligence. Scientists have tried to examine the relationship between sociality and complex cognition by comparing brain size with social group size. These studies have produced conflicting conclusions. A relationship between relative brain size and group size has been supported in mammals like primates (Barton 1996, Dunbar 1998), cetaceans (Marino 2002) and bats (Barton and Dunbar 1997), and insectivores and carnivores (Dunbar and Bever 1998). Yet this relationship has been more difficult to demonstrate in birds. For example, Beauchamp and Fernandez-Juricic (2004) found no relationship between non-breeding flock size and brain size in birds. Emery (2004) also found no correlation between social structure and brain size. Comparative work has produced conflicting evidence linking complex cognitive abilities with group size. Bond's group (2003, 2010) found that highly social pinyon jays were better at inferring the social dominance of unfamiliar birds using transitivity, than moderately social scrub jays. The same group (Bond et al. 2007) also found that highly social pinyon jays were better at serial reversal learning than moderately social scrub jays and asocial nutcrackers. Templeton, Kamil, and Balda (1999) compared social learning in nutcrackers and pinyon jays, and found that nutcrackers learned faster individually while pinyon jays learn faster socially. Some studies indicate that Clark's nutcrackers out-

perform other caching corvids in tests of spatial memory (i.e., Olson et al. 1995, Bednekoff et al 1997). However, in other studies (i.e. Gould-Beierle 2000, radial maze) nutcrackers did not out-perform pinyon jays and scrub jays, or even non-caching jackdaws. In a comparative study, pinyon jays demonstrated better spatial observational memory for caches made by other individuals, than did nutcrackers (Bednekoff & Balda 1996). The two comparative studies that were specifically designed to compare cache-protection (an indicator of social intelligence) among corvids both found that less social nutcrackers are sensitive to a conspecific observer, and adjust their behavior accordingly (the current study and Clary and Kelly 2011). Although findings from these comparative studies suggest that different cognitive processes (i.e. transitive inference, serial reversal, social learning, and cache-protection) may be governed by different constraints, it appears that group size does not solely predict complex cognitive abilities. Furthermore, since nutcrackers are considered food specialists and scrub jays are considered generalist foragers, I can also tentatively conclude that cache-protection may be a cognitive trait that is common to all caching corvids, regardless of group size or foraging type (generalism or specialism).

In light of my findings, I suggest that environmental pressures related to caching may have led to the development of a wide variety of cache-protection behaviors in corvid birds. Nutcrackers (genus *Nucifraga*) are most closely related to crows, ravens, and jackdaws (genus *Corvus*) (Erickson et al 2005). Phylogenies based on caching behavior indicate that nutcrackers (considered specialized cachers), and birds in the genus *Corvus* (considered moderate cachers), shared a recent common ancestor that was either a moderate or a specialized cacher (deKort and Clayton 2006). This common ancestor (or

an earlier one) may have developed increased social intelligence as an adaptive specialization to cope with the pressures of food hoarding and cache-protection. It is also possible that caching behavior and associated cache-protection strategies may have been lost and gained several times throughout evolutionary history. It is yet to be seen if other caching animals (like caching rodents) that also developed food hoarding through convergent evolution, also developed cache-protection strategies and advanced social intelligence. Thus it will be important to conduct comparative studies in closely related species in other groups of animals.

CHAPTER V

SUMMARY AND CONCLUSIONS

Summary of Background and Purpose

This research examined several cognitive abilities in the Clark's nutcracker. The Clark's nutcracker is a close relative of crows and ravens (Ericson et al. 2005), corvid birds which have been shown to possess many advanced cognitive abilities. Along with phylogenetic research, studies of social and caching behavior also suggest that these two genera (*Nucifraga* and *Corvus*) shared a recent common ancestor (Ekman & Ericson 2006, deKort & Clayton 2006, Figure 24). Thus, I was interested in examining whether this genetic relationship would predict that the nutcrackers in this study would demonstrate similar cognitive abilities as those seen in closely related corvids in past work. Also, the nutcracker possesses several unique ecological characteristics among corvids, which make them an important species to include in studies of cognition in corvids. For example, the nutcracker is the only species of corvid that lives in a high, cold, alpine habitat (900–3,900 m or 3,000–12,900 ft). Unlike other corvids, it is a specialist forager, which subsists mainly on the seeds of *Pinus* species (Lanner 1996). Also, they are thought to be the least social of the corvids (Templeton et al. 1999). Furthermore, although Clark's nutcrackers have been studied extensively for their remarkable spatial memory (they cache and recover astonishing numbers of pine seeds each autumn, Lanner 1996, Balda & Kamil 2006), little else is known about their

cognitive abilities.

Since the Clarks' nutcracker is the least social of the corvids, and the only species considered to be a specialist forager, it is an excellent species to include in comparative studies aimed at shedding light on the importance of socio-ecological factors like group size and foraging strategy in predicting complex intelligence. For example, scientists have posited that living in a large dynamic group drives the need for a large brain, and by extension, the development of complex cognitive abilities (Humphrey 1976, deWaal 1982, Jolly 1996, Barrett et al. 2002, Byrne & Whiten 1988 Owen 2009). There has been support for this idea in primates (i.e. lemurs, Jolly 1966), but additional research is needed to examine whether correlations exist across diverse groups of species between social complexity and individual "intelligence" (deWaal 1982). If these "social-intelligence hypotheses" are supported, the Clark's nutcracker, the least social of the corvids, should fall on the low end of the spectrum for "intelligence" among corvid birds. Others scientists have posited that foraging pressures are more important in driving complex cognition. For example generalist foragers, driven by the need to find and exploit various food resources, may have developed a wider cognitive repertoire than specialist foragers (Altshuler & Nunn 2001). Thus, if a generalist foraging hypotheses is supported, then the nutcrackers would be expected to be less proficient at solving problems than generalist foraging corvids. On the other hand, the nutcrackers heavy reliance on caching, recovering, and protecting food stores may have led these birds to develop unique cognitive abilities, as adaptive specializations for coping with these extreme foraging pressures.

In this body of work I examined cognitive abilities in Clark's nutcrackers, in three

diverse areas of cognition: 1) inferential reasoning by exclusion, 2) numerical cognition, and 3) social cognition. I selected these areas because (with a few exceptions) they have not been previously studied in nutcrackers. This research was expected to fill several gaps in the literature, and to address questions regarding the evolutionary origins of cognition in corvids, and perhaps, by extension, other groups of animals.

Inferential Reasoning by Exclusion

The first broad area of cognition I investigated was inferential reasoning by exclusion (Chapter II). Inferential reasoning by exclusion (also called exclusion performance or EP) is a specific type of reasoning, which has been defined as "the ability to select the correct alternative by excluding other alternatives" (Premack and Premack 1994). In Experiment 1, I used procedures that have been used previously to examine inferential reasoning in a variety of animals (i.e. primates, Call 2004; corvids Schloegl et al 2009, Schloegl 2011, Mikolasch et al 2011a and b). I trained several Clark's nutcrackers on a two-way object choice task, by baiting one of two containers with lids while a bird watched, and then allowing the bird to retrieve the food from the baited container. During testing, I baited one of the two containers out of sight, and then presented both containers, but showed the bird the contents of only the baited, only the empty, or neither of the containers (control). The critical test was the "empty" condition, in which the birds were shown the contents of only the empty container. In order to solve the problem, inferential reasoning by exclusion is thought to be required. That is, the thought process that may be necessary to solve the problem is such: if the food is not in this container I can exclude it as a choice, therefore I should select the other container. All of the birds were able to solve this problem immediately. When shown only an empty

container; they chose the other (baited container). However, it is possible that rather than using inferential reasoning to solve the problem, the birds could have simply avoided the empty cup (a simple associative mechanism).

To examine this possibility, I conducted another type of test (Experiments 2 and 3) that was less likely to be solved by associative processes (such as avoiding an empty vessel). The birds were trained that two distinctive objects were always found hidden in opaque containers, which were always positioned at the same two locations. During testing, one of the two objects was found in a transparent "trash bin", and was unavailable. To solve this problem, the birds had to infer that if one of the objects was in the "trash", then the other object should still be available in its previously learned hidden location. Only one out of the six birds tested was consistently able to make this inference (Experiment 3). This suggests that associative mechanisms likely accounted for my earlier results (i.e. the birds may have solved the initial problem by avoiding the empty cup. The failure of five of the six birds to solve the problem may have resulted from the difficulty of the task, a lack of motivation or attention to the critical features of the task by the other birds, or a failure to learn the role of the trash can. However, the fact that one bird was able to solve the more difficult task suggests that animals may be capable of using multiple mechanisms to solve problems of inference by exclusion. Indeed, the fact that most of the nutcrackers failed to solve the more complex inference tests may have resulted from their perseverance of using the same associative mechanisms that they used successfully in the initial task.

Several conclusions can be drawn from this study. The results from Experiment 1 are largely consistent with similar tests in two other seed-caching corvids, ravens

(Schloegl et al. 2009) and carrion crows (Mikolasch et al 2011a). However a non-caching corvid, the jackdaw, did not solve the task, choosing at chance when they could not see the food (Schloegl 2011). Since the nutcrackers demonstrated the ability to reason using inference, as well or better than ravens and other social caching corvids (and other social mammals), the results of this study do not support the idea that sociality drove the need for complex reasoning abilities (like the ability to make inferences). The fact that seed-caching nutcrackers performed similarly to other seed-caching corvids seems to indicate that inference by exclusion may have evolved as an adaptive specialization to the pressures of caching and recovering food (Mikolasch et al. 2011a, Kamil 1987, Shettleworth and Hampton 1998, deKort and Clayton 2006). Seed-caching birds may need to pay close attention to the absence or presence of food. This may have led to the development of inferential reasoning abilities in caching species (Mikolasch et al. 2011a). Thus the results of this study suggest that other factors (like foraging strategy or genetic relatedness) may be more important than sociality in predicting the ability of corvid birds to reason.

However, as pointed out previously, the procedure that has typically been used may not be the best way to test inferential reasoning, because the problem can be solved by a simpler mechanism. In Experiments 2 and 3 (inference with a trash bin) I used a novel paradigm, therefore I cannot compare the performance of nutcrackers with other corvids. The task I created may have been too difficult, or the training I used insufficient, such that the majority of birds could not solve the problem. Therefore, other birds (especially corvids and mammals) should be tested on this novel task to see if more animals can master the problem. Future work could also focus on honing the testing and

training procedures (beyond the basic task that has typically been used in the literature, and that I used in Experiment 1), to develop a more accurate way of examining inferential reasoning by exclusion, that can eliminate associative explanations.

Numerical Cognition

In Chapter III, I examined numerical cognition in nutcrackers, by testing their ability to discriminate between two different quantities of food. I used a two-way object-choice procedure, which has been used extensively to test relative quantity judgment in a wide variety of mammals. Because the nutcracker stores and recovers large numbers of pine nuts each season and has an exceptional spatial memory, I expected that this species might have enhanced number comprehension. To test this, I simultaneously presented the birds with two sets of nuts of different quantities, in 21 different comparisons (i.e. 1 nut *vs.* 2 nuts, 2 nuts *vs.* 3 nuts, up to 8 nuts *vs.* 16 nuts), to see if the mildly food deprived nutcrackers could choose the larger of the two quantities. The comparisons also varied with respect to the ratio of the two numbers. The nutcrackers successfully chose the larger of two quantities above chance in all but one of the 21 conditions I tested. The only condition the nutcrackers could not discriminate (above chance) was 8v9. The nutcrackers performance was consistent with Weber's law; the birds had more difficulty as the ratio of the two numbers in the comparison approached 1 (ratio effect), and they showed a slightly higher accuracy as the disparity between the two numbers increased (mild distance effect). They did not show a significant effect of magnitude, however; at constant distances, the birds did not have increasing trouble with larger contrasts (i.e. they did not have more difficulty with 4 *vs.* 5 than they had with 1 *vs.* 2).

I also ran three types of control tests, to determine which features the nutcrackers use to make their selections. The *Number* controls assessed whether the birds would choose by the number of objects, when the volume and area were both held constant. There were three *Number* control conditions, for example the nutcrackers were given a choice between 2 half nuts and 1 whole nut. I predicted that the birds would choose the larger number of nuts. However for the most part, they did not do so. Rather, they had a tendency to choose the side with the whole nuts rather than cut pieces when the volume (and approximate area) was the same. The *Volume* controls assessed whether the birds would choose by volume, when number and area were held constant. (i.e. choose 2 whole nuts over 2 half pine nuts). I predicted that they would be able to choose the larger volume when given these types of choices. As predicted, the nutcrackers consistently demonstrated the ability to discern which pile had the larger volume of "nut material". The *Area* controls, assessed whether the birds would choose by area when number and volume were held constant. Here the birds were given a choice between two piles of nuts with the same volume and number (i.e. 3 nuts spaced close together versus 3 nuts spaced farther apart). I predicted that the birds would choose the larger array, because they would consider the larger array to have more food. On the contrary, the birds mostly chose the side where the food covered a smaller area.

The results from the controls tests are consistent with an optimal foraging model, in which animals behave as if to maximize energy intake. The results from the *Number* controls (i.e. the birds' preference for 1 whole nut over 2 half nuts) suggest that the nutcrackers were able to recognize that the two choices held equivalent volumes of food. Thus the birds demonstrated a preference for unbroken food when the total volume was

held constant. The birds did not make a common mistake made by young children, who tend to think that 2 is more than 1 without regard to total volume. Rather, they behaved more like adult humans (i.e. Geier et al. 2006). In the *Volume* controls, the nutcrackers had no problem discriminating the larger of two volumes when number was held constant (i.e. a preference for 2 whole nuts over 2 half nuts). This is logical, as animals should be able to choose a pile that has a larger volume of food over a pile that has the same total number of items but a lesser volume. In the *Area* controls, the nutcrackers chose the array with the smaller area (i.e. they chose 2 nuts spaced close together over 2 nuts spaced farther apart). This may be an exhibition of foraging efficiency. In general, animals may be hardwired to choose food that is closely packed, to save energy in harvesting. On the other hand, this ability is not innate in small human children, who incorrectly choose a large array over small array, even when both contain the same number of items. Older children eventually lose this misconception. Thus, the performance of the nutcrackers in this study is more similar to that of post pre-operational children than to that of younger children.

In this study, the nutcrackers demonstrated numerical abilities that may exceed the abilities of many large brained social mammals (including apes and young children). Here the nutcrackers selected the larger of two simultaneously presented sets of food, for set sizes up to 16, whereas most mammals (except dolphins, elephants and African gray parrot) have been limited by a set size of about 4. Similar to many of the mammals tested previously, the nutcrackers appear to behave according to Weber's law, showing decreased performance as the ratio between the two numbers approaches 1 (ratio effect), and an slight increase in performance as the numbers increased in disparity (distance

effect). However, another common effect seen in mammals is the magnitude effect (which states that at constant distances larger numbers are more difficult to discern), was not seen in the nutcrackers in this study.

My results also suggest that the nutcrackers use an analog magnitude system to represent numbers, in which larger numbers are represented in a fuzzy way. The use of an analog magnitude system has also been suggested for a few large-brained social mammals (i.e. elephants and dolphins). The other representational system that has been suggested for mammals is the object-tracking (or object-file) system, which allows animals to hold individual numbers in a sort of "filing cabinet" with limited number of "slots". Scientists have suggested that the use of an object-file system may explain why many mammals (including primates) are limited to discriminating numbers up to about four. The results of this study do not support the use of an object-file representational system by nutcrackers.

Similar tests have not been previously conducted in other corvids, so a comparative analysis is not possible. Nevertheless, some preliminary explanations for the results of this study can be postulated. Since the nutcrackers demonstrated number competence on par or exceeding that of social animals, it does not appear that living in a large social group drove the need for complex numerical abilities. Rather, other evolutionary pressures (i.e. the need to keep track of large numbers of stored seeds, or number of seeds in a cache) may have driven the need for numerical abilities in nutcrackers and other animals. The nutcracker may have developed a keen number sense as an adaptive specialization to cope with their unique ecological pressures (i.e. intense food-hoarding). It also seems likely that enhanced number abilities may be tied to long-

term or spatial memory, as both may be controlled by the same brain areas (hippocampus Krebs et al. 1989, Sherry et al.1989, Basil et al. 1996; intraparietal sulcus Dehaene 1997). However, more tests are needed to examine numerical ability in nutcrackers and related corvids (as well as other animals that do and do not store food), to shed light on which pressures drive the evolution of numerical cognition.

Social Cognition

Chapter IV was specifically designed as a direct test of social intelligence hypotheses. Here, I replicated a series of studies that were aimed at comparing social intelligence in the highly social scrub jay (Dally et al 2004 and 2005a), and the less social Clark's nutcracker. Specifically, I wanted to know if nutcrackers, like scrub jays, use cache-protection behaviors flexibly when an observer (potential pilferer) is present. I set up a caching arena and an adjacent cage that could hold a conspecific observer (observed condition), or remain empty (private condition). I placed a bowl of 50 pines the nutcrackers in the arena, and gave the nutcrackers a 15 minute period in which they could eat or cache in one of two locations (trays filled with corn cob filings) in the arena. Twenty-four hours later, I gave the birds a 5 minute recovery period, to find and eat or re-cache any nuts they had cached the day before. I conducted various tests to determine if the nutcrackers alter their caching behavior when an observer is present.

In Experiment 1, the caching trays were arranged so that that one was near the observer's cage and the other one was farther away. Here I found that when the nutcrackers were observed making caches, they cached significantly more nuts in the far tray compared to the near tray. They also cache significantly fewer nuts in the near tray when they cached with an observer than they cached in a tray that was near an empty

cage (private condition). In Experiment 2, the birds did not alter their caching or recovery behavior with regard to a "sunny" or a "shady' tray when they were observed caching; thus they do not appear to use the cache-protection strategy of caching in dimly lit location. In Experiment 3, I examined the nutcrackers caching decisions, by giving them a choice to cache behind a visual barrier that obstructed the view of the caching site from the observer, or in a site that was in plain view of the observer. When given a choice, the nutcrackers reduced caching in the tray that was located in-view of the observer (compared to the amount of caching in that tray in private). Furthermore, the birds recovered more nuts from the in-view tray when they had been observed making the caches than they recovered when they had cached in private. Next, I gave the nutcrackers experience both pilfering and having their own caches pilfered to see if this would serve to increase cache-protection. There was no difference in behavior before and after the pilfering-experience.

In an additional analysis (Experiment 4), I examined whether caching efficiency might be altered when an observer is present. Using videos from the visual barrier experiment (Experiment 3), I scored the number of pecks to each tray, and calculated caching frequency by dividing the number of nuts cached by the number of pecks made to that tray. I also scored the amount of time spent near each tray, and calculated caching rate by dividing the number of nuts cached by the amount of time spent near that tray. When they were observed caching, the nutcrackers increased both caching frequency and caching rate in the hidden tray. The birds spent a great deal of time pecking in the in-view tray without caching there. Next, I wanted to determine whether the birds were exhibiting territorial aggression or true cache-protection behavior (Experiment 5). To

examine this, I repeated Experiment 3 (Visual Barrier) with the food removed from the caching arena. I then compared the amount of time spent in each area of the caching arena when food was present and when food was absent. The nutcrackers spent more time near the in-view tray than near the hidden tray in both cases, but they spent significantly more time near the in-view tray when food was present than when food was absent. The results from this experiment (combined with the results from Experiment 4) strongly suggest that the nutcrackers were exhibiting cache-protection behavior directed at the in-view tray when they were observed; for example guarding their caches, trying to intimidate the observer, or even making false caches to confuse the observer. As far as I am aware, this is the first empirical study to demonstrate this behavior among corvid birds.

The results from this direct comparison of caching behavior in the relatively asocial nutcrackers and the more social scrub jay (Dally et al. 2004, 2005a), has allowed me to draw some conclusions about the role of social group size (and the role of caching) in predicting social intelligence. Foremost, because the nutcrackers demonstrated some cache-protection behaviors that are similar to more social scrub jays, (as well as some unique behaviors), the results of this study do not support social intelligence hypotheses. Cache-protection strategies that both nutcrackers and scrub jays (Dally et al. 2005a) demonstrated include caching far from an observer, and recovering more from near and in-view locations when they had been observed. Like nutcrackers, scrub jays also increase caching rate (number of nuts/sec) when they are observed. However, unlike scrub jays (Dally et al. 2004), which prefer to cache in the shade when observed, the nutcrackers did not show a preference to cache in a dimly lit location (as

opposed to a brightly lit location). Another difference is that scrub jays increased the amount of caching (number of nuts) when they were observed, while nutcrackers did not increase (or suppress) caching in the presence of the observer. The nutcrackers simply cached (and recovered) more nuts (in all conditions, both observed and private) than scrub jays did. This is likely due to their larger size and the possession of a sublingual pouch. Also it is likely that evolutionary pressure from increased reliance on stored seeds led to their proficiency at caching and recovery. Also, unlike scrub jays (Dally et al. 2005a), the nutcrackers in this study did not increase cache-protection behavior after pilfering-experience. Thus, these wild-caught nutcrackers may have been innately sensitive to the presence of a conspecific observer and altered their behavior accordingly, or they may have learned and remembered from experiences they had years ago, prior to capture. Since both nutcrackers and scrub jays cache food, the results of this study suggest that ecological pressures of caching or having a common ancestor that developed the cognitive capacity to alter one's behavior to protect food from conspecifics, may predict this type of social intelligence.

Limitations

There were several limitations of this collective body of work. Foremost, this work was limited by the inclusion of data from a very small number of animals. Testing a larger number of birds will be important to verify the results obtained in this study. Furthermore, the nutcrackers used in this study have been in captivity for a long period of time, and their age at capture is unknown. Thus, differences in age among individuals might be a factor that can explain why some birds succeeded while others failed at various tasks. The sex of the birds is also unknown; therefore individual differences in

behavior that were demonstrated in these experiments may be attributed to innate differences in behavior between males and females. Differences in individual learning history of the birds (prior to capture) may also have impacted the results obtained here. Because the birds have been in the laboratory for a long time, they have been exposed to several types of experiments prior to testing in this study. These experiences may have altered the nutcrackers' behavior, making interpretation of my results more difficult. Likewise, this artificial experience may render a comparison with the behavior of wild birds invalid. For example, the fact that birds had been housed together, and may recognize each other, might have affected the results in the social cognition experiments (Chapter IV). Thus, these experiments should be repeated using a larger number of hand-raised birds (of known sex and age) with known and potentially limited prior experience. It would also be interesting to repeat these experiments in a wild population of birds, to see how their behavior would compare with the behavior of these captive birds. Comparisons with birds from other laboratories (i.e. scrub jays) should be interpreted cautiously because of differences in learning history in animals that were raised in different laboratories. Ideally, multi-species comparative research would be conducted in the same laboratory.

Conclusions

Collectively, the results from these three cognitive studies in the Clark's nutcracker, suggest several conclusions. First, the cumulative results of this research do not seem to support social intelligence hypotheses (i.e. social function of intellect, Humphrey 1976), at least for corvid birds. Even though they are the least social of the corvids, the nutcrackers demonstrated inferential reasoning and social intelligence on par

with more social corvids (i.e. ravens, crows, scrub jays). The exact numerical tests I used here have not been conducted in other corvids, so it is entirely possible that other corvids may exceed the abilities of nutcrackers in this realm. This is unlikely though, as jackdaws and ravens were limited by a set size of about 6 or 7 using a different paradigm (Koehler 1951). Thus, it seems that group size is not an important predictor of complex cognition, as least not for corvids and the types of cognition examined here.

The social-brain hypothesis is also not supported by my results. In recent years, there have been over 50 comparative analyses of social and ecological variables that have been used to explain variation in whole brain size (vertebrates, Healy and Rowe 2007). Results from individual studies have produced conflicting evidence about whether a correlation exists between brain size (corrected for body size) and various cognitive traits. For example, Lefebvre and colleagues (2002) found that in widely-divergent groups of birds, cognitive processes (i.e. tool use) were correlated with large brains. However, due to large difference in methodology (data collection and analyses) there have substantial problems interpreting what brain size means (Pravosudov and deKort 2005). The Clark's nutcracker has a total brain mass of 5.3g (Miklovsky 2003). The nutcrackers total brain volume/body size ratio is neither the smallest nor the largest among corvids (extrapolated from Garamszegi and Eens 2004); yet their performance was on par with corvids with larger brain/body ratios, for most of the tasks in three broad areas of cognition in which they were tested in this research. This suggests that total brain volume/body size is not a good predictor of complex cognition.

Others have looked at specialized parts of the brain, and tried to correlate these with various types of cognitive behavior. For example, the adaptive specialization

hypothesis predicts that food-caching birds should have an enlarged hippocampus and better spatial memory compared to non-caching species (Pravosudov and deKort 2005). However although many studies support this premise (Krebs et al. 1989, Sherry et al. 1989, Healy and Krebs 1992, Basil et al. 1996,Garamszegi and Eens 2004), Brodin and Lundborg (2003) failed to find a significant relationship between food-caching behavior and hippocampal volume. Pravosudov and deKort (2005) also found discrepancies among correlations of hippocampal volume and food-caching propensity. Thus, they strongly suggest that more data are needed "to justify generalizations about brain evolution in birds and to avoid possible spurious correlations". It was once believed that the Clark's nutcracker possesses the largest hippocampal volume/ body size ratio among caching corvids, (Garamszegi and Eens 2004), and this was thought to be causally related to their exceptional spatial memory. However, differences in methodology (i.e. different storage methods for tissues used in analyses, etc) for measuring hippocampal volume have now caused scientists to question this idea (Pravosudov and deKort 2005). I performed a simple comparison of data taken from Garamszegi and Eens (2004), who claim to have found a significant correlation between caching and hippocampal volumes. However, the data therein do not seem to support the idea that nutcrackers (which rely most heavily on caching) have a larger hippocampal volume/body mass ratio compared with other corvids that rely less heavily on caching (i.e. nutcrackers 44.7 mm^3/130.8 g= **2.926**; carrion crows 136.8 mm^3 /417g = **3.05**; scrub jays 24.9 mm^3/75.5 g = **3.03**; taken from Garamszegi and Eens 2004). Interestingly the hippocampus is important for spatial memory, and some scientists believe that this area may also control numerical cognition (i.e. Dehaene, 1997). If this were true, it could explain why nutcrackers, which have

exceptional spatial memory (i.e. Kamil & Balda 1985, Gibson & Kamil 2001a and b, Gibson & Shettleworth 2003), demonstrated such extreme proficiency at discriminating different number combinations in the current research. In any case, scientists are beginning to conclude that looking at whole brain size or the size of various brain parts may not be the most useful way to predict which complex cognitive traits are likely to be present in a given species. Perhaps it would be more beneficial to examine neural density in certain regions of the brain, as opposed to looking at the overall size of the brain. It would also be sensible to examine entire neural networks instead of focusing on individual brain areas.

My data can be used to examine several ecological hypotheses aimed at understanding factors which may influence the development complex cognition in a species. For example, the ecological-intelligence hypothesis, which predicts that generalist foragers should develop a wider cognitive repertoire than specialist foragers (Altshuler & Nunn 2001), is not supported by my findings. The Clarks' nutcracker, a highly specialized forager, demonstrated cognitive abilities that are similar to other generalist foraging corvids. On the other hand, the extractive foraging hypothesis (Parker & Gibson 1977), which states that difficulty extracting foods from their casing (i.e. nuts) may drive the need for complex intelligence (Gibson 1986), may be supported by these data. Clark's nutcrackers rely on the seeds of pine trees, which must be pried out of a pine cone. These birds use their beak in a precise manner like a needle-nose pliers, to retrieve the nuts from deep within the cone. The birds typically cache the nuts with the shells intact. Then upon retrieval, the nuts must be carefully manipulated to crack the hard outer shell and remove a papery film from around the actual pine seed. This the

birds do very deftly, sometimes by standing on the nuts and using their beaks to remove the seed, which is usually extracted in one piece (personal observation). Other corvids may also rely on nuts and other foods that are difficult to extract, thus they may have developed a large cognitive repertoire. Another possibility, the ephemeral food supply hypothesis, which states that food sources that are scarce, seasonal, or patchy, require extra cognitive capacities to monitor their availability (Clutton-Brock and Harvey 1980, Milton 1981), could also be supported by my findings. Clark's nutcrackers (and perhaps other corvid species) must keep track of pine nuts which are seasonal; in fact they have increased pressure to do so, as this food source becomes unavailable during harsh winters at high altitudes. Furthermore, these nuts decay easily if left exposed too long, so after extraction the birds need to cache them fairly quickly (and they must be able to keep track of when and where they were cached). Similarly, the cognitive mapping hypothesis (Milton 1988) states that the pressures of locating patchily distributed but potentially predictable food sources may drive complex cognition (due to the need for a mental representation of the environment). This hypothesis may also be supported in nutcrackers and other corvids.

It seems likely that caching behavior and the need to protect caches from pilferage may drive the need for complex cognitive abilities, like keeping track of who is watching and where, and altering one's behavior flexibly. However, many animals that do not cache food (i.e. chimpanzees Call 2004) also demonstrate similar cognitive abilities. Furthermore some animals that do store food may not demonstrate these abilities. Thus, food caching cannot be the sole predictor of complex cognition. It will be important to test more caching corvids and other groups of food-hoarding animals to see if cognitive

abilities like social intelligence and the ability to reason are present, and to help us decipher which factors predict them. Future work could focus on comparative cognitive experiments with seed-caching rodents (i.e. chipmunks, rats, hamsters, gophers), other caching bird species (i.e. chickadees, woodpeckers), and perhaps even food-hoarding invertebrates (i.e. ants, spiders, crabs). Another distinct possibility is that many factors, such as food-caching and protection, a patchily distributed or seasonal food supply, difficulty of food extraction (and others traits like pair-bonding, long developmental period, etc.) work in combination to cause an organism to develop complex cognitive skills.

Since the Clark's nutcrackers in this study demonstrated cognitive abilities similar to closely related corvids like ravens, crows, and scrub jays, a major implication of this research is that a common ancestor of the caching corvids may have developed these cognitive traits (reasoning abilities, number competence, and social intelligence) as adaptive specializations, and subsequently passed them on to the Clark's nutcracker and other extant caching corvids. For example, on a simple test of inferential reasoning by exclusion (Chapter II, experiment 1), the nutcrackers performance was similar to that of ravens and carrion crows. However, ravens and crows have not yet been tested on a more difficult task that rules out associative mechanisms (like the one I used in Chapter II, Experiment 3). If ravens and crows solve the more difficult problem, like one individual nutcracker in this study did, then I can conclude that the common ancestor of birds in the genera *Nucifraga* and *Corvus* (Figure 24) or an even earlier predecessor may have developed the ability to reason using inference by exclusion. To determine if an earlier ancestor also possessed this cognitive trait, inferential reasoning could be tested in other

close relatives like magpies (*Pica pica*, a non-caching corvid) and scrub jays (*Aphelocoma*). In another example, nutcrackers performed similarly to scrub jays in tests of social intelligence (cache-protection behavior), thus the ancestor common to both (Figure 24), or an earlier ancestor, may have developed these abilities as a strategy to cope with cache-pilferage. It would be very interesting to test more distantly related caching corvids, like gray jays (genus, *Perisoreus*) to see if they also use cache-protection behavior flexibly. Furthermore, it will be important to test ravens and scrub jays (as well as more distant caching and non-caching relatives, like magpies *Pica pica*) on closely replicated numerical discrimination tasks (Chapter III) to determine if number sense is linked closely with caching or other behavioral traits, and to determine if the split between birds that possess these traits and those which do not occurred farther back in evolutionary history. We may be able to pinpoint a common ancestor that developed these abilities (social, inferential, numerical); however the fact that these traits could have been gained and lost many times presents challenges. Another potentially fruitful line of research would be to replicate my studies (in these several areas of cognition) in the only other member of the genus *Nucifraga*, the Eurasian or spotted nutcracker (*Nucifraga caryocatactes*). This species lives in a different habitat, at lower altitudes, but still caches and relies on pine nuts for survival. Though there is a good deal of information about the natural history of this species, I am not aware of any cognitive testing that has been conducted as of yet. Thus it would helpful, from a comparative standpoint, to examine which ecological factors differ among these two nutcracker species (*N. columbiana* and *N. caryocatactes*), to help inform us about which factors are important for these traits to develop. In any case, it is clear that much more comparative work is needed.

Although the main goal of this research was to compare the performance on several cognitive tasks between the asocial Clark's nutcrackers and more social corvids (and other social animals), the work herein is not truly comparative in the sense that none of the studies examined multiple species. Ideally, comparative experiments such as this should be conducted with several related species in the same laboratory. In this way, the learning history of the animals, as well as the exact methodological procedures to be used can be better controlled. However, truly comparative studies using multiple species are rare. Obtaining and maintaining a large population of animals of numerous species requires a great deal of space, money, and time. For many laboratories, these constraints are prohibitory. Therefore, more funding is needed for truly comparative work, which will help us to answer questions about the evolutionary underpinnings of cognition in animals, and ultimately help us understand the unique cognitive traits that have arisen in humans.

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APPENDIX A

Condition	Sony	Puck	Starr	Betsy	Susan	Total Number correct out of 40	Total % correct
	Number correct out of 8	Number correct out of 8	Number correct out of 8	Number correct out of 8	Number correct out of 8		
1v2	8*	7*	8*	7*	4	34*	85*
1v3	6	7*	5	6	5	29*	72.5*
1v4	8*	7*	8*	7*	8*	38*	95*
1v5	7*	8*	8*	6	7*	36*	90*
2v3	6	7*	6	6	3	28*	70*
2v4	7*	8*	4	7*	5	31*	77.5*
2 v5	6	7*	6	3	7*	29*	72.5*
3v4	5	6	7*	5	2	25*	62.5*
3v5	8*	7*	4	7*	6	32*	80*
3v8	7*	8*	4	6	7*	32*	80*
4v5	6	7*	3	5	4	25*	62.5*
4v6	8*	7*	7*	7*	7*	36*	90*
4v8	4	6	7*	7*	7*	31*	77.5*
5v6	3	7*	6	5	7*	28*	70*
6v7	6	7*	7*	6	5	31*	77.5*
6v8	5	5	7*	5	6	28*	70*
6v9	7*	8*	5	6	5	31*	77.5*
6v12	6	4	6	6	3	25*	62.5*
8v9	5	4	6	4	4	23	57.5-NS
8v10	5	8*	4	5	7*	29*	72.5*
8v16	7*	7*	6	6	7*	33*	82.5*
Total % correct	77.4	84.5	73.8%	72.6	69.0		

Table 1. Binomial probabilities for individual birds (and totals) in each condition. "Correct" means the subject chose the larger of the two numerosities in the condition. A * indicates performance significantly different than chance ($P < 0.05$).

	Sony	Puck	Starr	Betsy	Susan	Total out of 40	Total %
	Total # larger out of 8	**Total # larger out of 8**	**Total # larger out of 8**	**Total # larger out of 8**	**Total # larger out of 8**		
Number controls							
1Lv2S	4	1*	2*	4	3	14*	35* sm
2Lv4S	3	1*	3*	2*	3	12*	30* sm
3Lv6S	5	1*	4	2*	4	16	40-NS
Total % larger number	50	12.5	37.5	33.3	41.7		
Volume controls							
1Lv1S	7*	8*	7*	7*	8*	37*	92.5*
2Lv2S	8*	8*	7*	8*	7*	38*	95*
3Lv3S	7*	8*	6	8*	7*	36*	90*
Total % larger volume	91.7	100	83.3	95.8	91.7		
Area controls							
2Cv2F	2*	2*	3	3	2*	12*	30* sm
3Cv3F	3	3	3	3	6	18	45-NS
4Cv4F	5	3	3	6	4	21	52.5-NS
Total % larger area	41.7	33.3	37.5	50	50		

Table 2. Binomial probabilities for individual birds (and totals) in the *Number*, *Volume*, and *Area* controls. A * indicates performance significantly different than chance ($P < 0.05$).

APPENDIX B

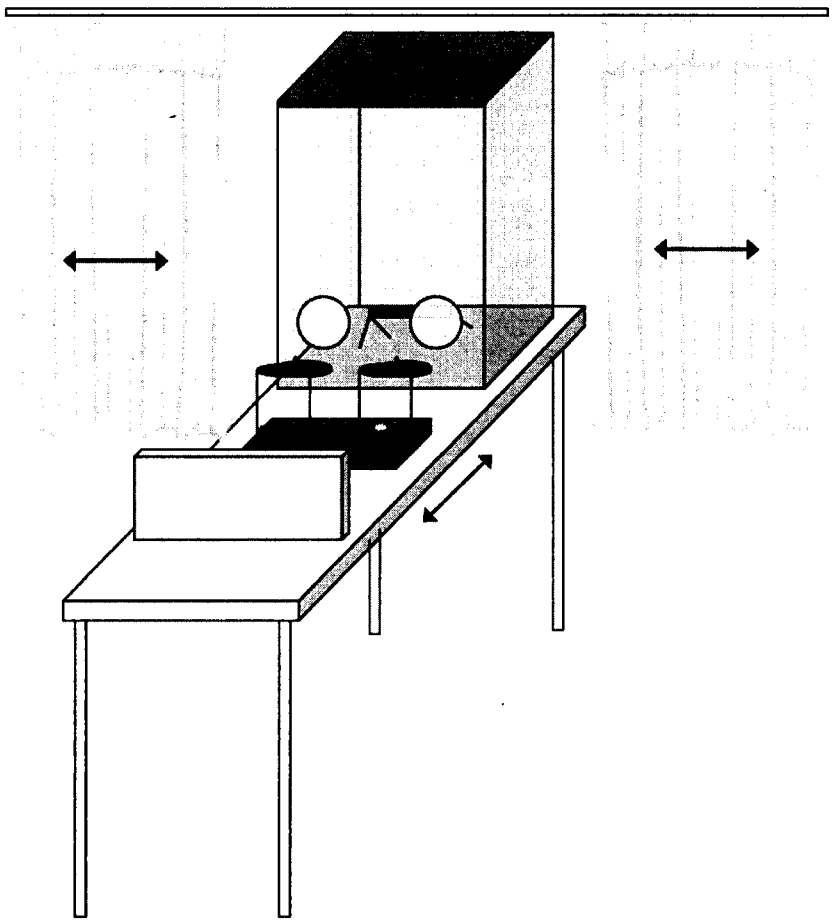

Figure 1. Experimental apparatus for two-way object choice task.

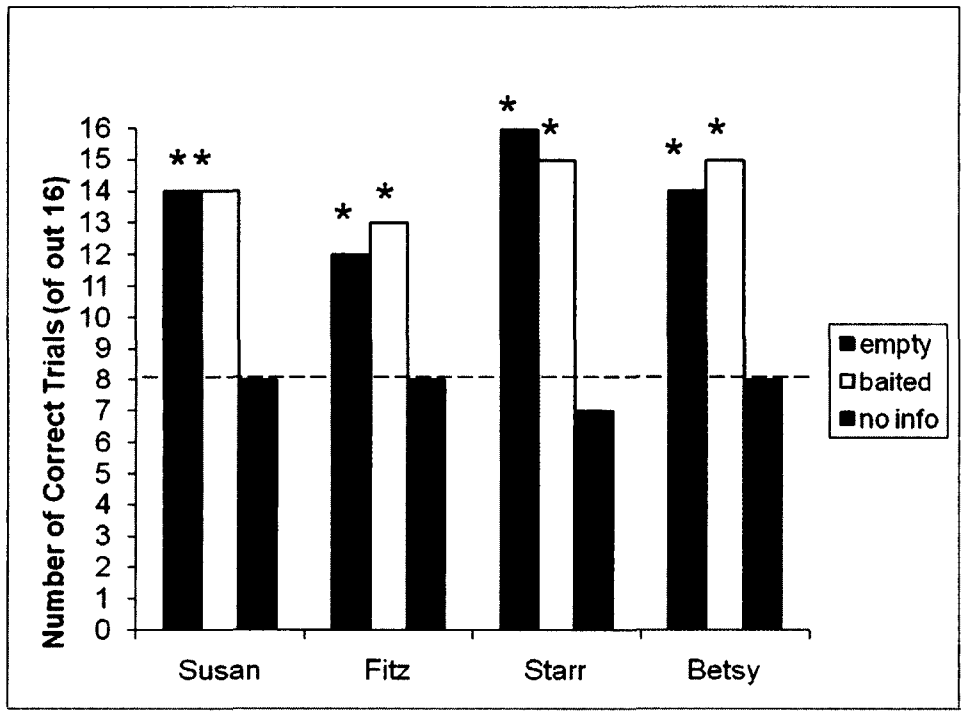

Figure 2. Results for Experiment 1, all three conditions. Number of correct choices (choosing the baited cup) out of sixteen are shown for each bird in each condition. A * indicates performance significantly above chance ($P < \alpha_{obt}$).

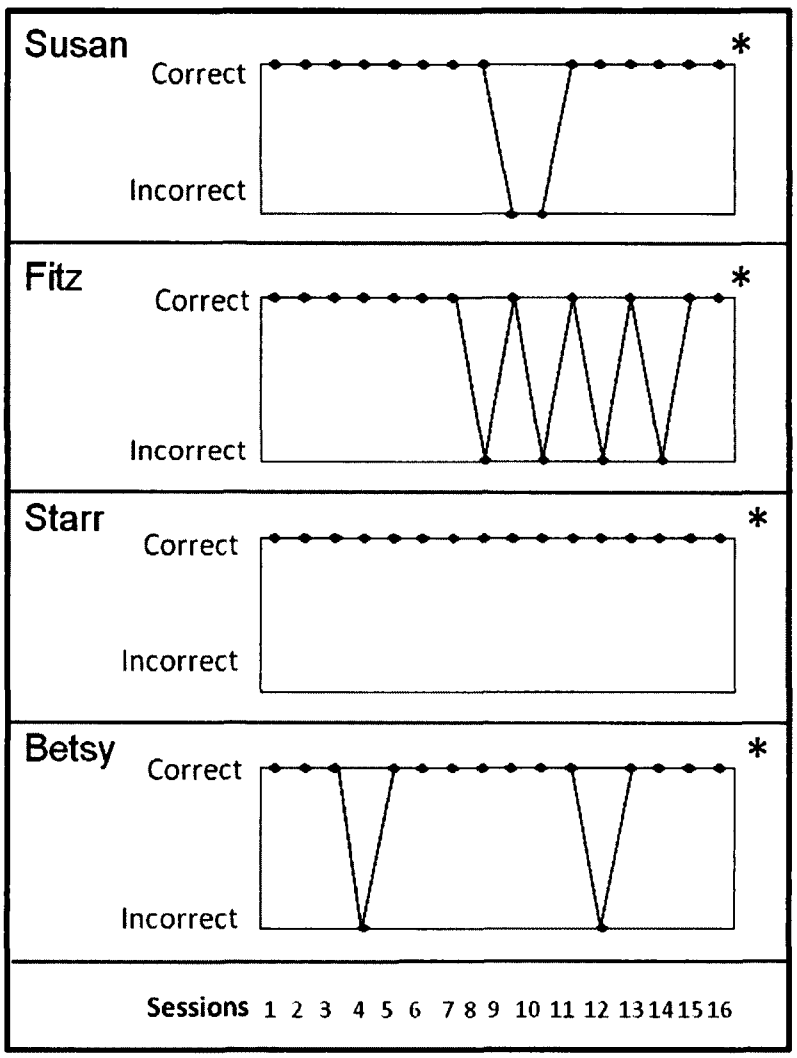

Figure 3. Results for Experiment 1 (empty condition), raw data from individual birds showing correct and incorrect choices across sessions. For example, Susan chose correctly during the first session and seven subsequent sessions. Note that Starr chose correctly in 16 out of 16 sessions. A * indicates performance significantly above chance ($P < \alpha_{obt}$).

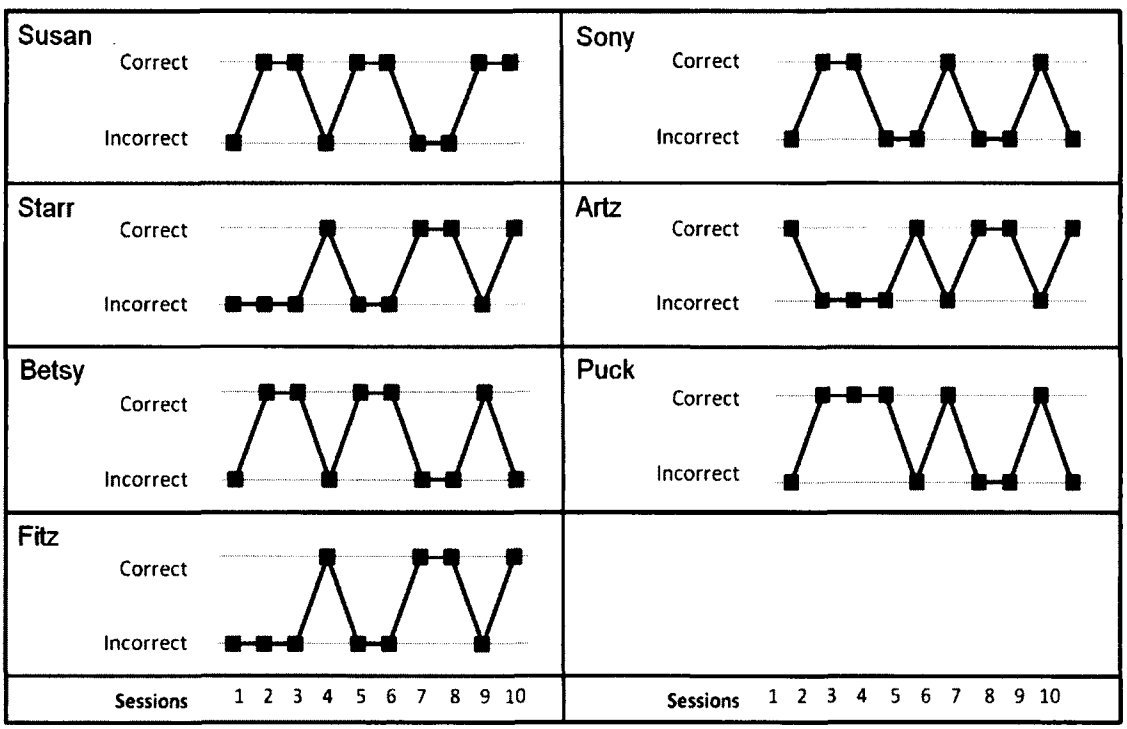

Figure 4. Results for Experiment 2, raw data for each bird across sessions. The birds choices were random, that is, they did not significantly chose the food type that was still available (all $P > \alpha_{obt}$).

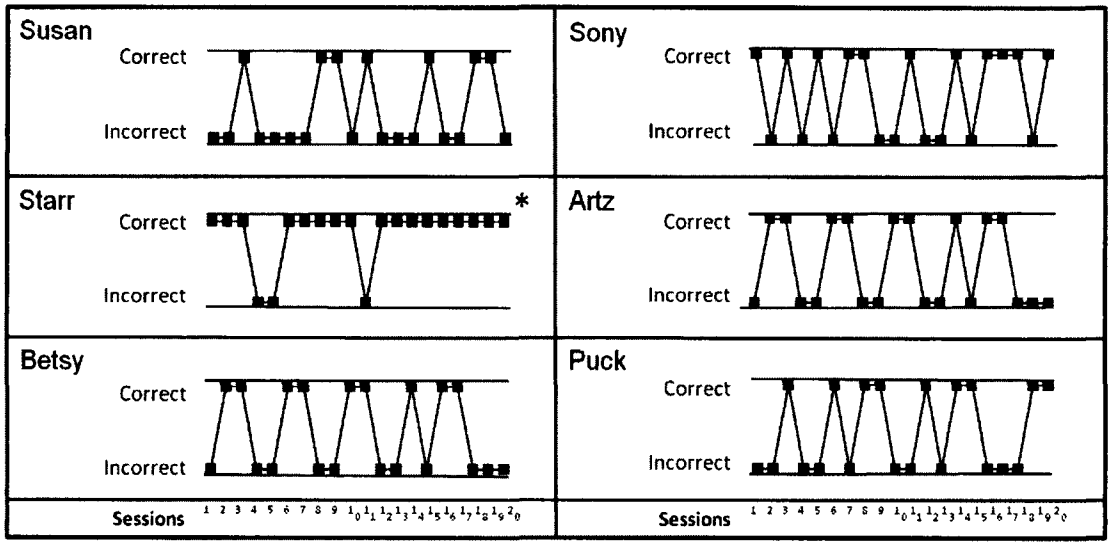

Figure 5. Results for Experiment 3, raw data for each bird across sessions. One bird (Starr) consistently chose the toy that was not in the "trash" (a * indicates performance significantly above chance, where $P < \alpha_{obt}$).

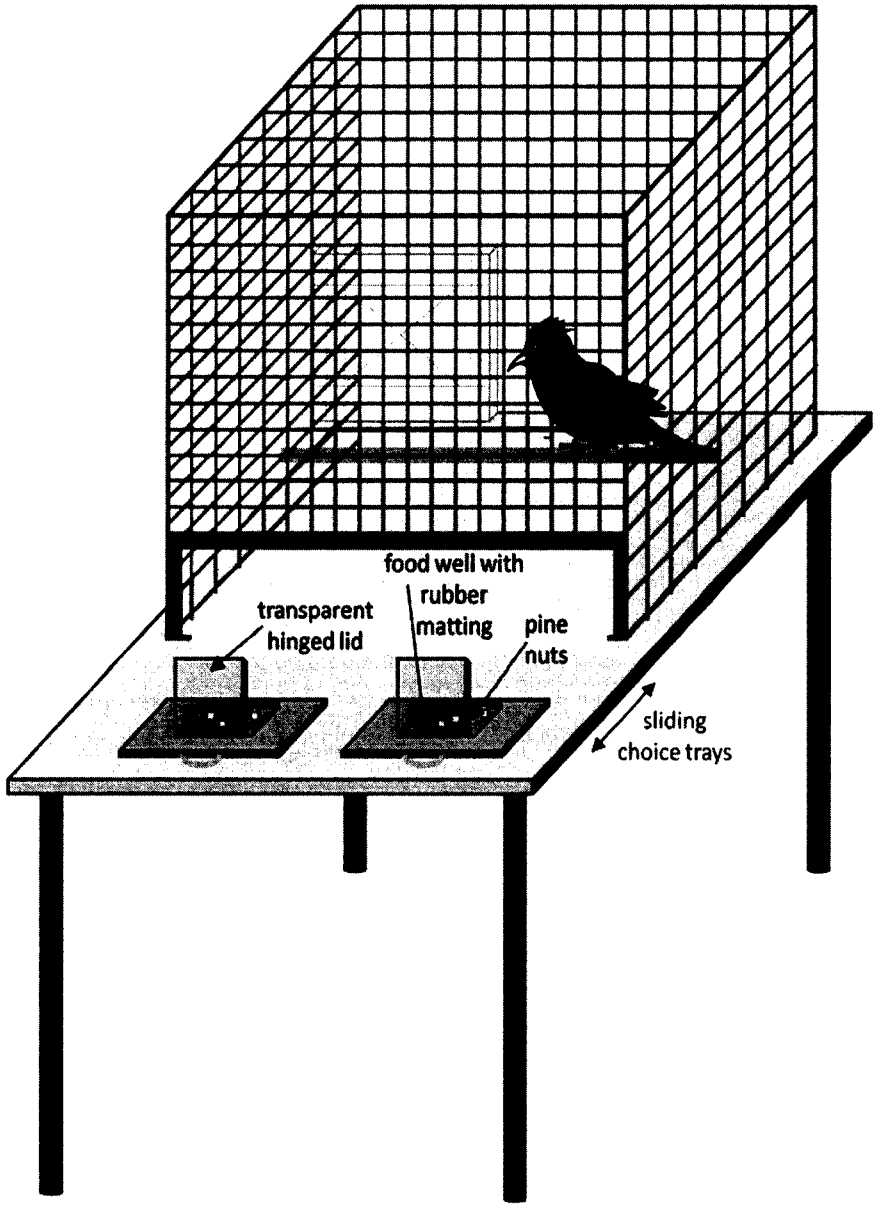

Figure 6. Experimental apparatus for number discrimination task.

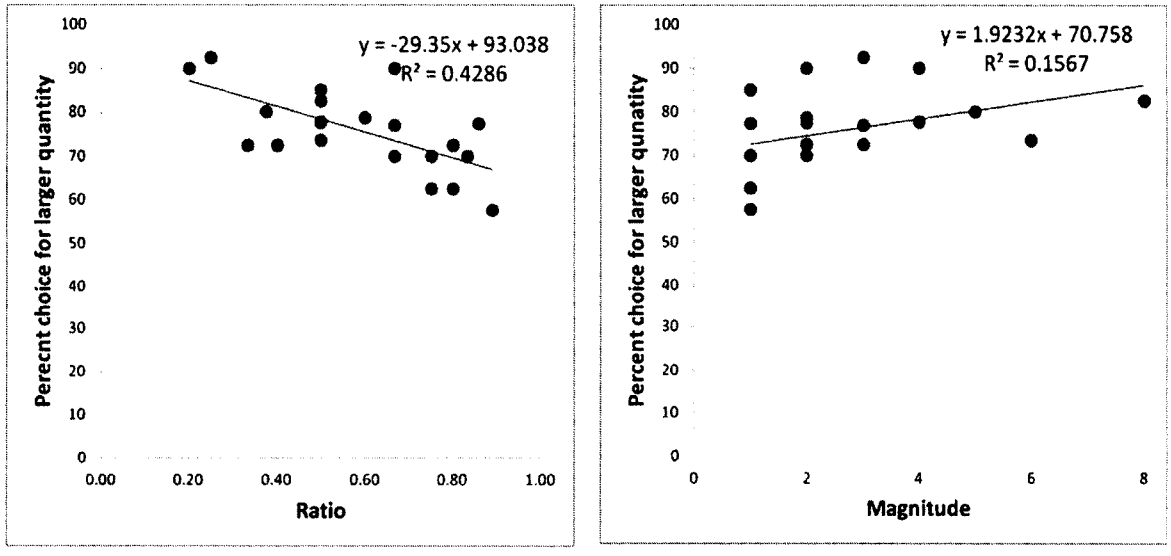

Figure 7. Regression showing the effects of ratio and distance (Weber's law). The nutcrackers had more difficulty as the ratio of the two quantities to be discriminated increased (approached 1). Performance improved as the distance between the two quantities increased, but this was not a significant effect.

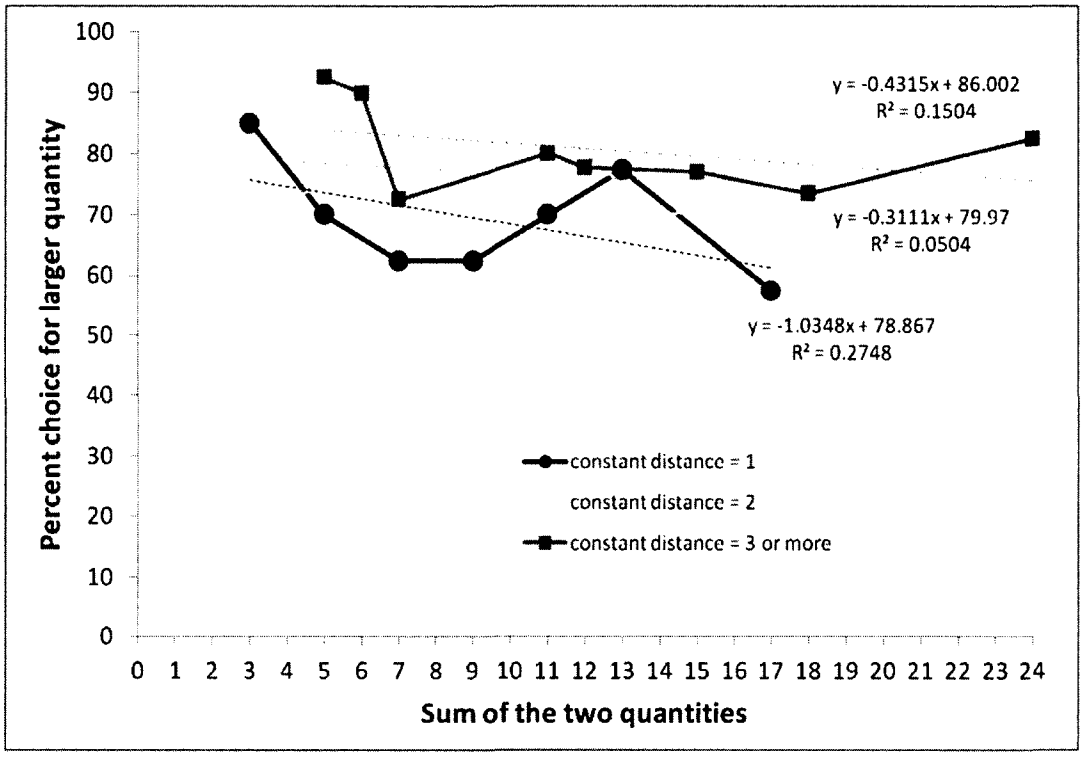

Figure 8. Regression showing the effect of magnitude. There is no significant effect of magnitude; at constant distances (binned into constant distances of 1, 2, and 3 or more), the nutcrackers discriminated large contrasts just as easily as small contrasts.

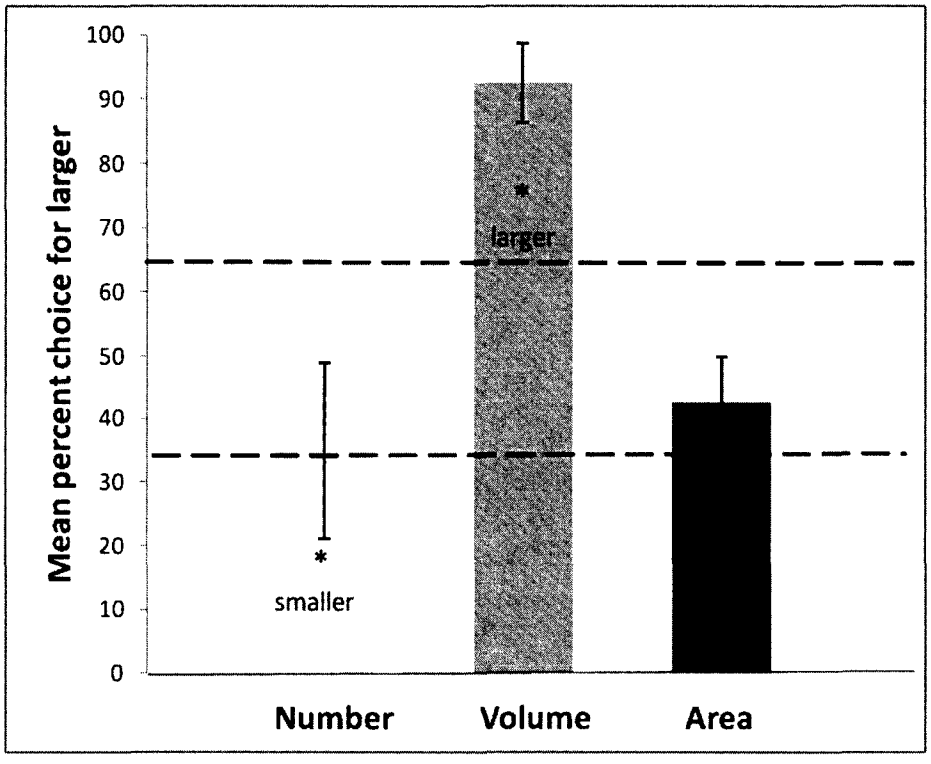

Figure 9. Pooled results from the *Number*, *Volume*, and *Area* controls.

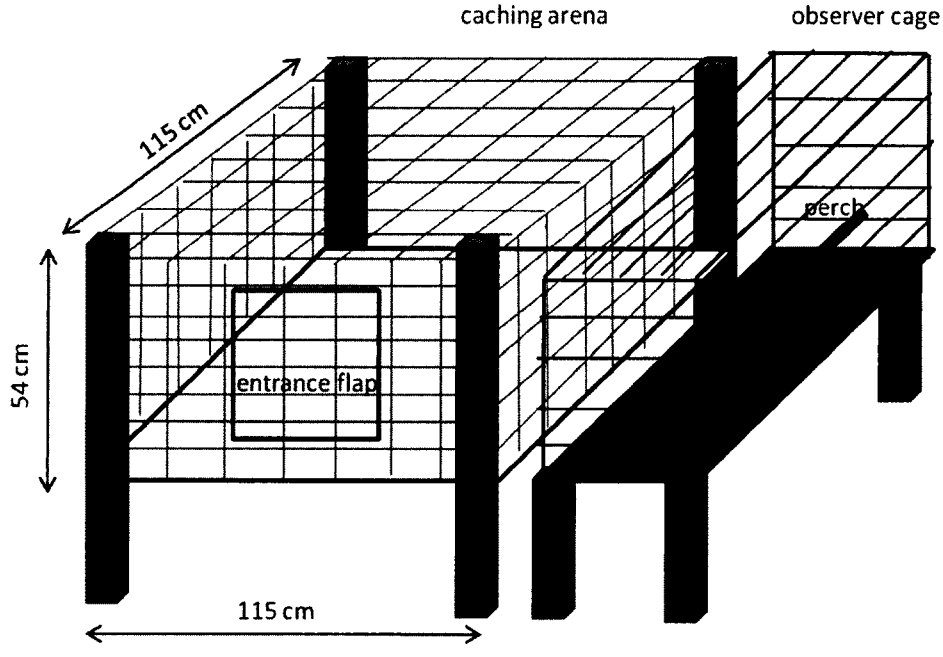

Figure 10. Experimental apparatus for cache-protection study

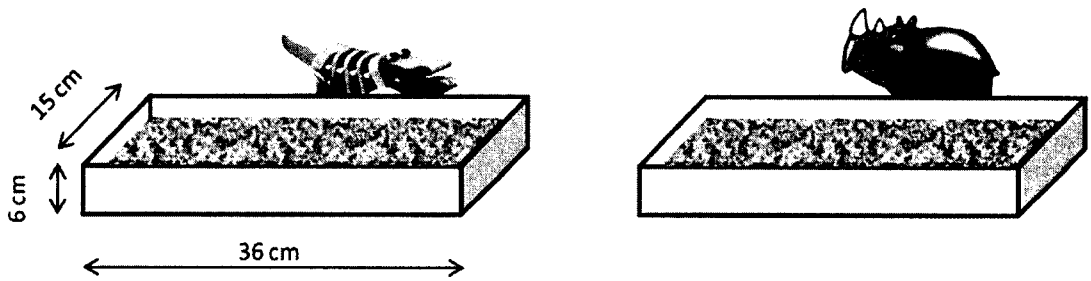

Figure 11. Caching trays.

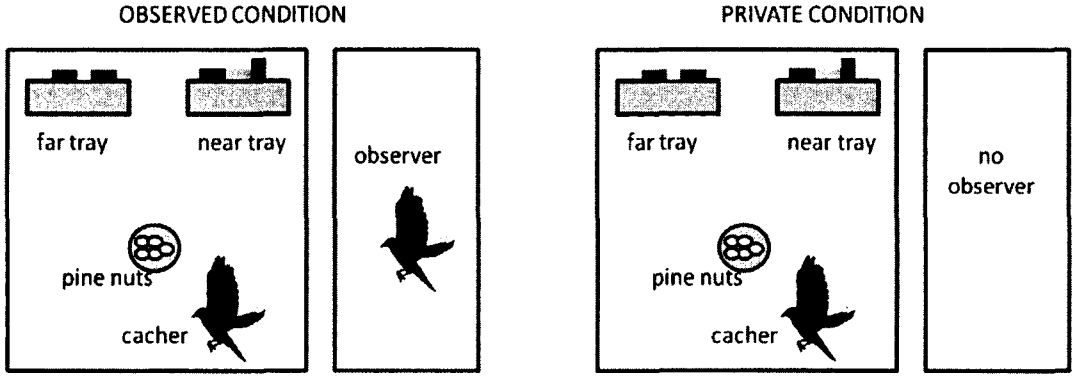

Figure 12. Setup for Experiment 1 (Effect of Distance).

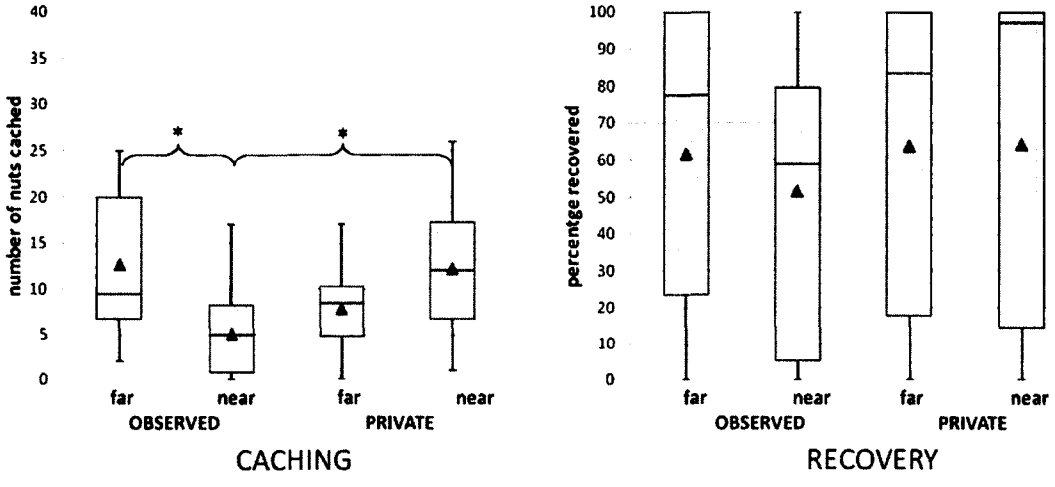

Figure 13. Results for Experiment 1 (Effect of Distance); caching (left panel) and recovery (right panel). These box plots show the median, 25th percentile and 75th percentile of the number of nuts cached (out of 50) and the proportion of nuts recovered. The error bars indicate minimum and maximum values. The ▲ represents the mean number of nuts cached or the mean proportion of nuts recovered. Data are pooled across birds. A * indicates a significant difference among groups (paired *t*-tests with Bonferroni correction).

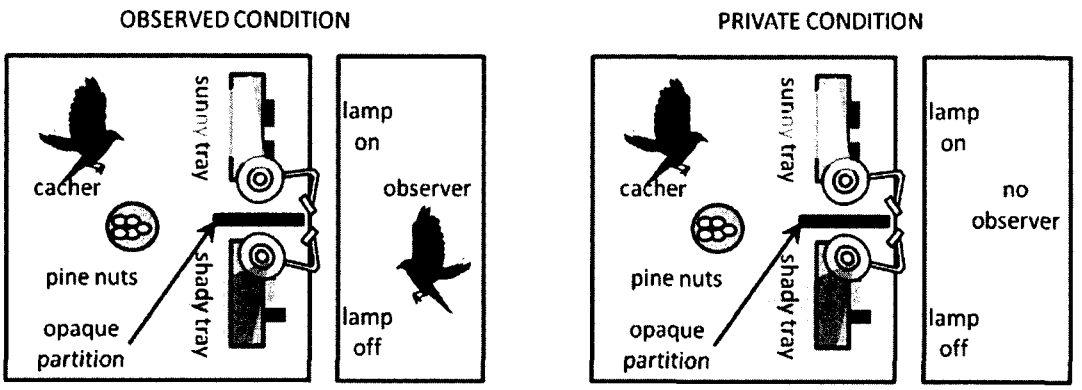

Figure 14. Setup for Experiment 2 (Effect of Lighting).

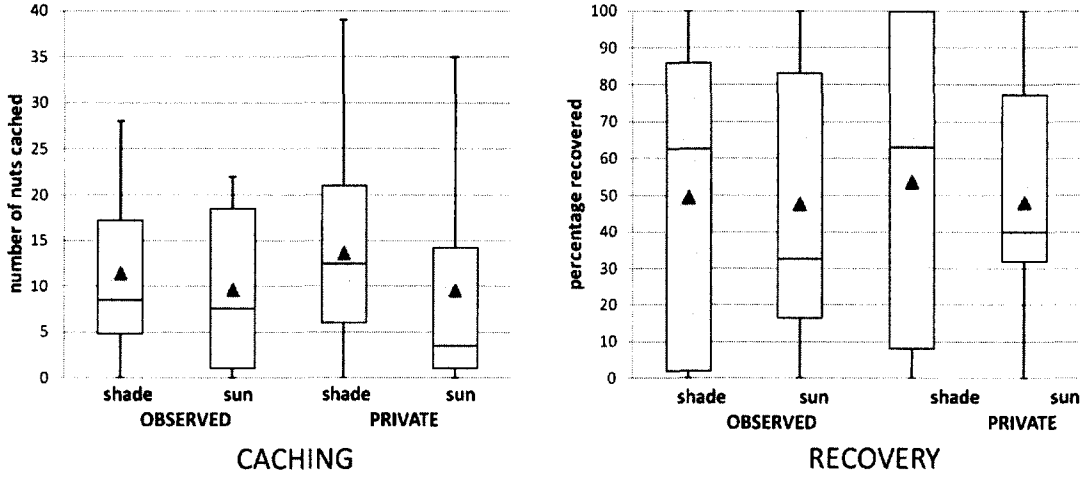

Figure 15. Results for Experiment 2 (Effect of Lighting); caching (left panel) and recovery (right panel). Median, 25th percentile and 75th percentile of number of nuts cached (out of 50) and recovered (proportion of nuts cached) are shown. The error bars indicate minimum and maximum values. The ▲ represents the mean number of nuts cached. Data are pooled across birds. There were no significant differences among groups (paired *t*-tests with Bonferroni correction).

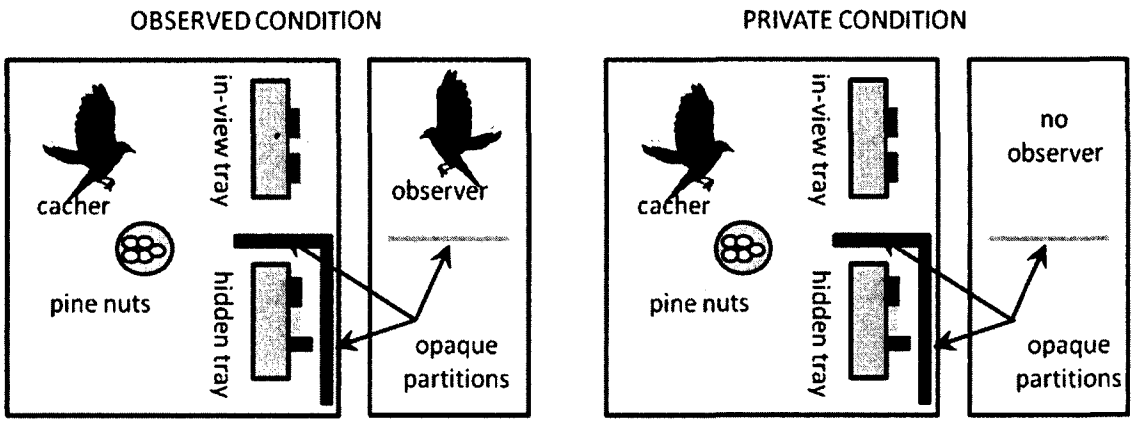

Figure 16. Setup for Experiment 3 (Visual Barrier).

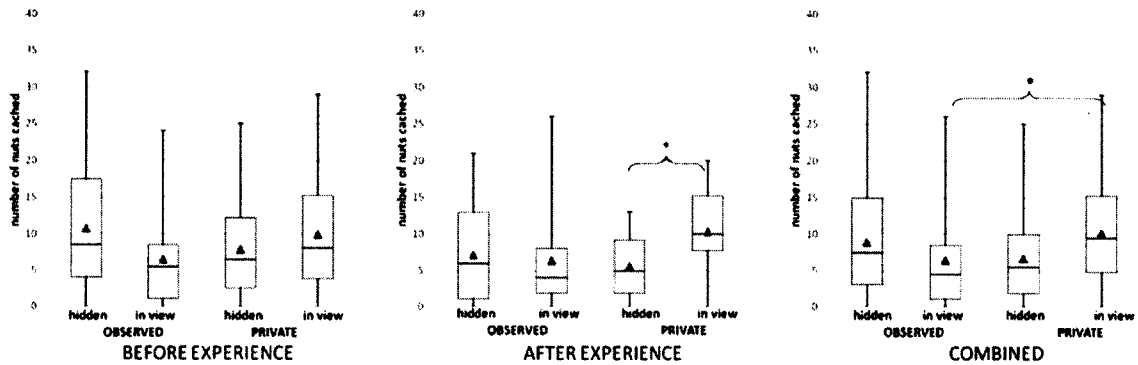

Figure 17. Results for Experiment 3 (Visual Barrier); caching before (left panel) and after (middle panel) pilfering experience. The right panel shows the combined caching data from before and after pilfering experience. The box plots show the median, 25th percentile and 75th percentile of number of nuts cached (out of 50). The error bars indicate minimum and maximum values. The ▲ represents the mean number of nuts cached. Data are pooled across birds. A * indicates a significant difference among groups (paired *t*-tests with Bonferroni correction).

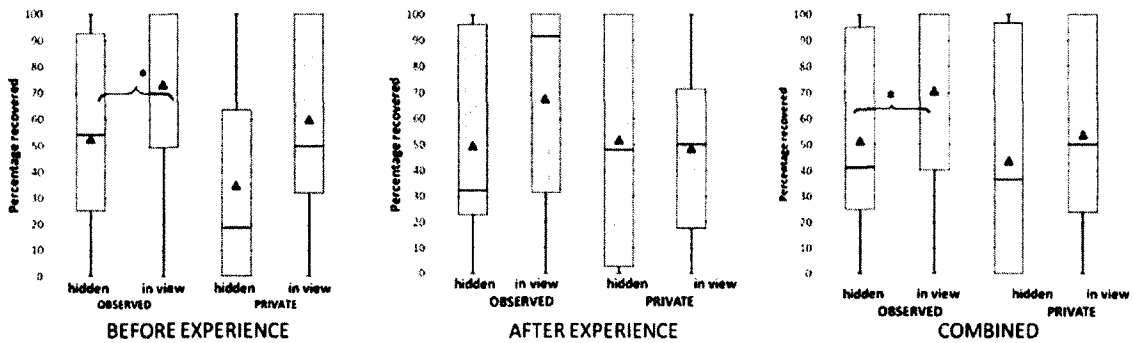

Figure 18. Results from Experiment 3 (Visual Barrier); recovery before (left panel) and after (middle panel) pilfering experience. The right panel shows the recovery data from before and after pilfering experience combined. Median, 25th percentile and 75th percentile of nuts recovered (after a 24-hour retention period) are shown. The error bars indicate minimum and maximum values. The ▲ represent the mean proportion of nuts recovered. Data are pooled across birds. There were no significant differences among groups (paired *t*-tests with Bonferroni correction).

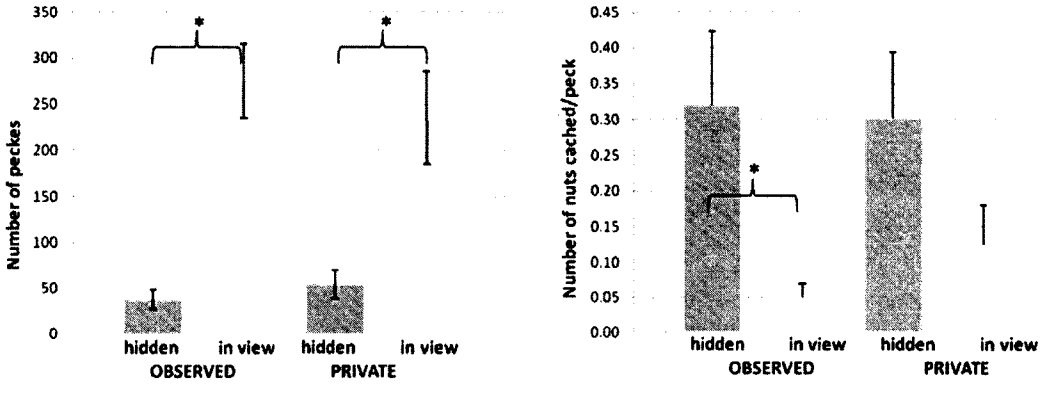

Figure 19. Results from Experiment 4 (Number of pecks and caching frequency). In the visual barrier experiment, the nutcrackers pecked more in the in view trays, but they cached significantly more nuts per peck in the hidden side when observed compared to the in view side (more efficient). They pecked more without caching in the in-view tray (which may indicate false-caching). A * indicates a significant difference among groups (paired *t*-tests $P < \alpha_{obt}$).

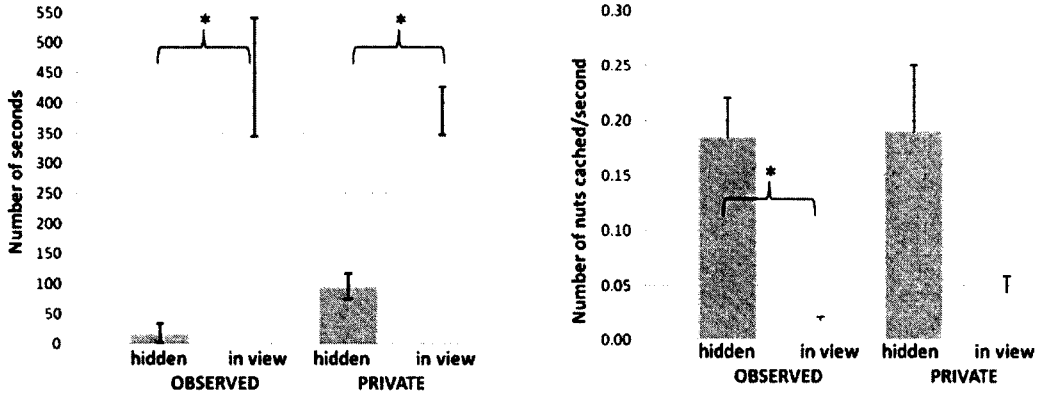

Figure 20. Results from Experiment 4 (Time spent and caching rate). In the visual barrier experiment the nutcrackers spent more time near the in-view trays, but they cached significantly faster in the hidden side when observed compared to in private (more efficient). A * indicates a significant difference among groups (paired *t*-tests P $< \alpha_{obt}$).

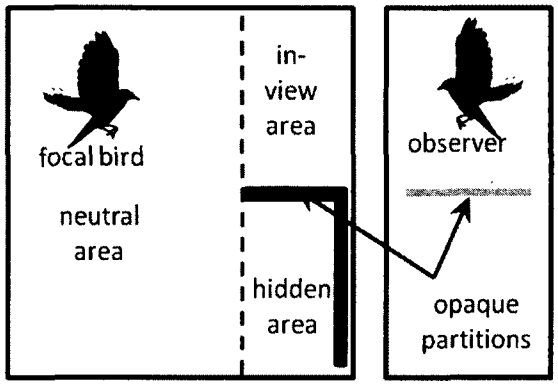

Figure 21. Setup for Experiment 5 (Control for social interactions). I divided the arena into three sections, and videotaped social interactions in the absence of food. I calculated the amount of time spent in each of the three sections in 15 minute sessions, and adjusted this time for the relative size of the section.

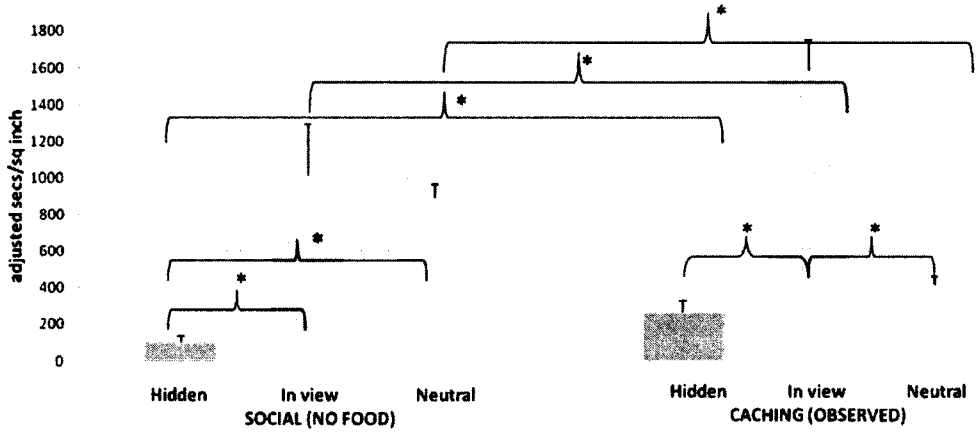

Figure 22. Behavior in the presence and absence of food. Proportion of time spent in each of three sections of the arena in 15 minute social sessions (no food) was compared with time spent in these sections during caching sessions, when food was present. A * indicates a significant difference among groups (planned comparisons two-tailed paired *t*-tests, $P < 0.05$). The nutcrackers the largest proportion of time near the in-view tray when they were observed and food was present, suggesting cache-guarding or false caching behavior.

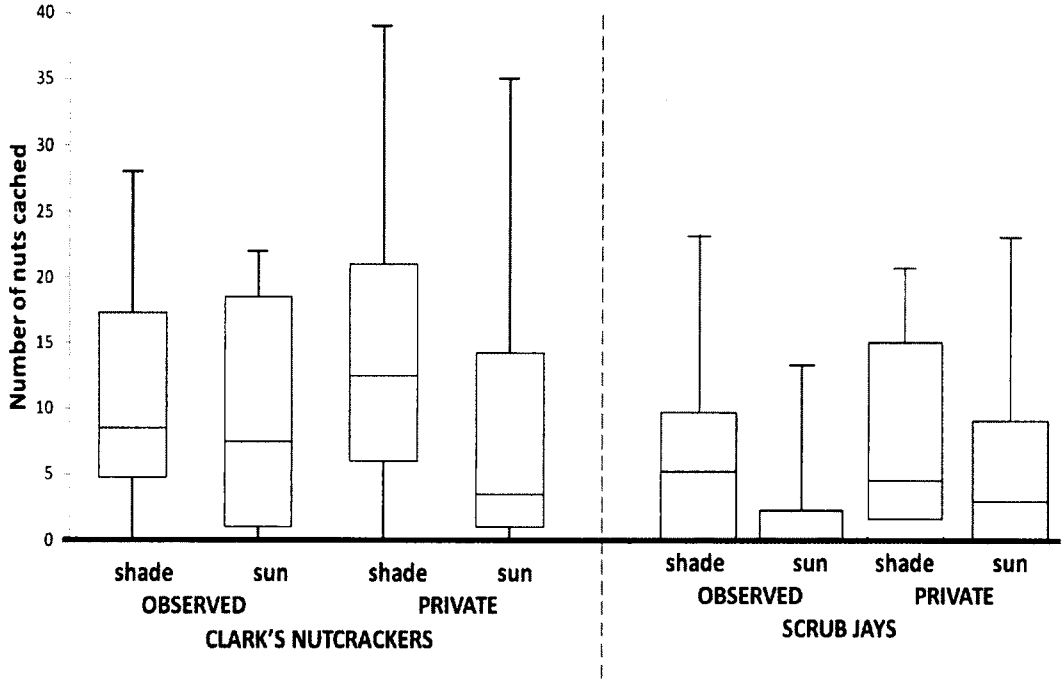

Figure 23. Comparison of the number of nuts cached by asocial nutcrackers and social scrub jays. Median, 25th percentile and 75th percentile of pine nuts cached (in a 15 minute period) are shown. The error bars indicate minimum and maximum values. Data are pooled across birds. Generally, the nutcrackers cached a larger number of nuts than scrub jays. The nutcrackers also recovered (24 hours later) a larger percentage of nuts that they had cached compared to scrub jays (not shown). Scrub jay data were reproduced with permission (Dally et al. 2004).

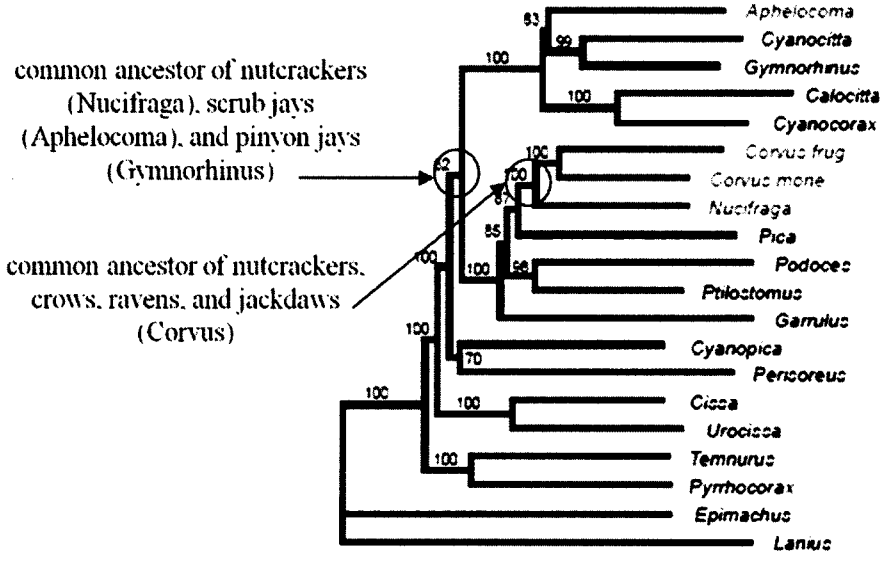

Figure 24. Phylogenetic tree (based on three genes) resulting from a maximum likelihood analysis (reproduced in part, with permission from Erikson et al. 2005).

APPENDIX C

University *of* New Hampshire

Research Conduct and Compliance Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

October 24, 2007

Brett Gibson
Psychology, Conant Hall
Durham, NH 03824

IACUC #: 071004
Project: Inferential reasoning in the Clark's nutcracker (Nucifraga columbiana)
Category: B
Approval Date: 19-Oct-2007

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category B on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the study involves either no pain or potentially involves momentary, slight pain, discomfort or stress.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Roger Wells at 862-2726 or Julie Simpson at 862-2003.

For the IACUC,

Jessica A. Bolker, Ph.D.
Chair

cc: File

University of New Hampshire

Research Integrity Services, Service Building
51 College Road Durham, NH 03824-3585
Fax: 603-862-3564

24-Mar-2011

Gibson, Brett M
Psychology, Conant Hall
Durham, NH 03824

IACUC #: 110303
Project: Numerical Cognition in the Clark's Nutcracker
Category: C
Approval Date: 23-Mar-2011

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.* The IACUC made the following comment(s) on this protocol:

1. In Section VII, C, #21 and #22, the IACUC checked "No."
2. The committee noted that documentation of numerical intelligence in this species would represent a significant new finding.
3. Is it worth testing bigger quantity distinctions as well (e.g., 2v10)?
4. Will the birds recognize powdered pine seeds as food?

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
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If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jessica Bolker

Jessica A. Bolker, Ph.D.
Chair

cc: File
Tornick, Jan

University of New Hampshire

Research Integrity Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

17 Jun 2010

Gibson, Brett M
Psychology, Conant Hall
Durham, NH 03824

IACUC #: 100604
Project: Cache protection and prospection by the Clark's nutcracker, Nucifraga columbiana
Category: D
Approval Date: 16-Jun-2010

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gail Porsche, UNH Health Services.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jessica A. Bolker, Ph.D.
Chair

cc: File